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C. A. MENÉNDEZ

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FOSSIL BENNETTITALES FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

BY

CARLOS ALBERTO MENÉNDEZ

(Museo Argentino de Ciencias Naturales, Buenos Aires)

Pp. 1–42 ; 19 *Plates ;* 91 *Text-figures*

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In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

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TRUSTEES OF
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FOSSIL BENNETTITALES FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

By CARLOS ALBERTO MENÉNDEZ

SYNOPSIS

This paper deals with the Bennettitales of the Ticó fossil flora located 160 km. north-west of Port San Julian in the Province of Santa Cruz, Argentina. The group is represented by seventeen species of which thirteen are new; they are referred to seven genera (*Otozamites*, *Dictyozamites*, *Ptilophyllum*, *Pterophyllum*, *Zamites*, *Williamsonia* and *Cycadolepis*). All the species, except *Ptilophyllum hislopi*, were found with cuticle preserved.

The fossil plants described indicate in general an age between Upper Jurassic and Lower Cretaceous. On the basis of all the known species so far recorded in the Ticó flora a Wealden age may be postulated.

I INTRODUCTION

THE material described in this paper was collected at Ticó and adjacent areas, approximately in 48° 50′ S. lat. by 69° W. long., nearly 160 km. north-west from the Port of San Julian in the Province of Santa Cruz, Argentina.

The flora was discovered by Dr. J. M. de Giusto, geologist of Yacimientos Petrolíferos Fiscales, and sample impressions on a coarse dark grey sandstone were sent to me by Dr. T. Suero for study. In subsequent excursions undertaken by Dr. S. Archangelsky and the writer, new deposits were found containing specimens with preserved organic remains. The organic remains consist of epidermal cuticles and integuments of seeds, spores, etc. some of which were preserved in such a way that they could be studied microscopically without previous treatment. In a few cases the carbonized parts of the wood parenchyma were also preserved. Brief maceration of the material with nitric acid and potassium chlorate followed by ammonia was all that was necessary to obtain good clean preparations and these were mounted in glycerine jelly.

The preservation of the plants is not the same in all the deposits. In some no cuticle is preserved and the impression of the plant on a tufaceous clay or coarse sandstone is all that remains.

The numerous outcrops in the area contain abundant plant remains which belong to a rich flora and a complete study of the material will demand extensive research. Some of the conifers, six fern-like fronds and a small fruit, have already been described and figured by Archangelsky (1963) as a first contribution to the knowledge of this flora. The following species were described: *Ticoa harrisii* Arch., *T. magnipinnulata*

Arch., *Ruflorinia sierra* Arch., *Mesodescolea plicata* Arch., *Mesosingeria coriacea* Arch., *M. herbstii* Arch., *Ktalenia circularis* Arch., *Brachyphyllum brettii* Arch., *B. mucronatum* Arch., *B. mirandai* Arch., male cones associated with *B. mirandai*, *B. irregulare* Arch., *Athrotaxis ungeri* (Halle) and *Tomaxellia degiustoi* Arch.

With only partial knowledge of this rich flora it has not yet been possible to determine its exact age, but a preliminary consideration of the possible age, based on the fossils now known, is given at the end of this paper.

II SYSTEMATIC DESCRIPTIONS

BENNETTITALES

Genus *OTOZAMITES* Braun

Otozamites parviauriculata sp. nov.

(Pl. 1, figs. 1–3 ; Pl. 2, figs. 7, 8 ; Text-figs. 1–7)

DIAGNOSIS. Leaf up to 4·5 cm. wide, narrower below ; pinnae up to 23 mm. × 7 mm., and at an angle of about 80° to the rachis, varying from slightly separated to slightly overlapping. Pinna margins nearly parallel, shape slightly curved to make the obtuse apex point somewhat forwards ; attachment by middle of basal margin, auricle very little developed. Veins radiating almost symmetrically from region of attachment, forking to maintain a concentration of about 35 per cm.

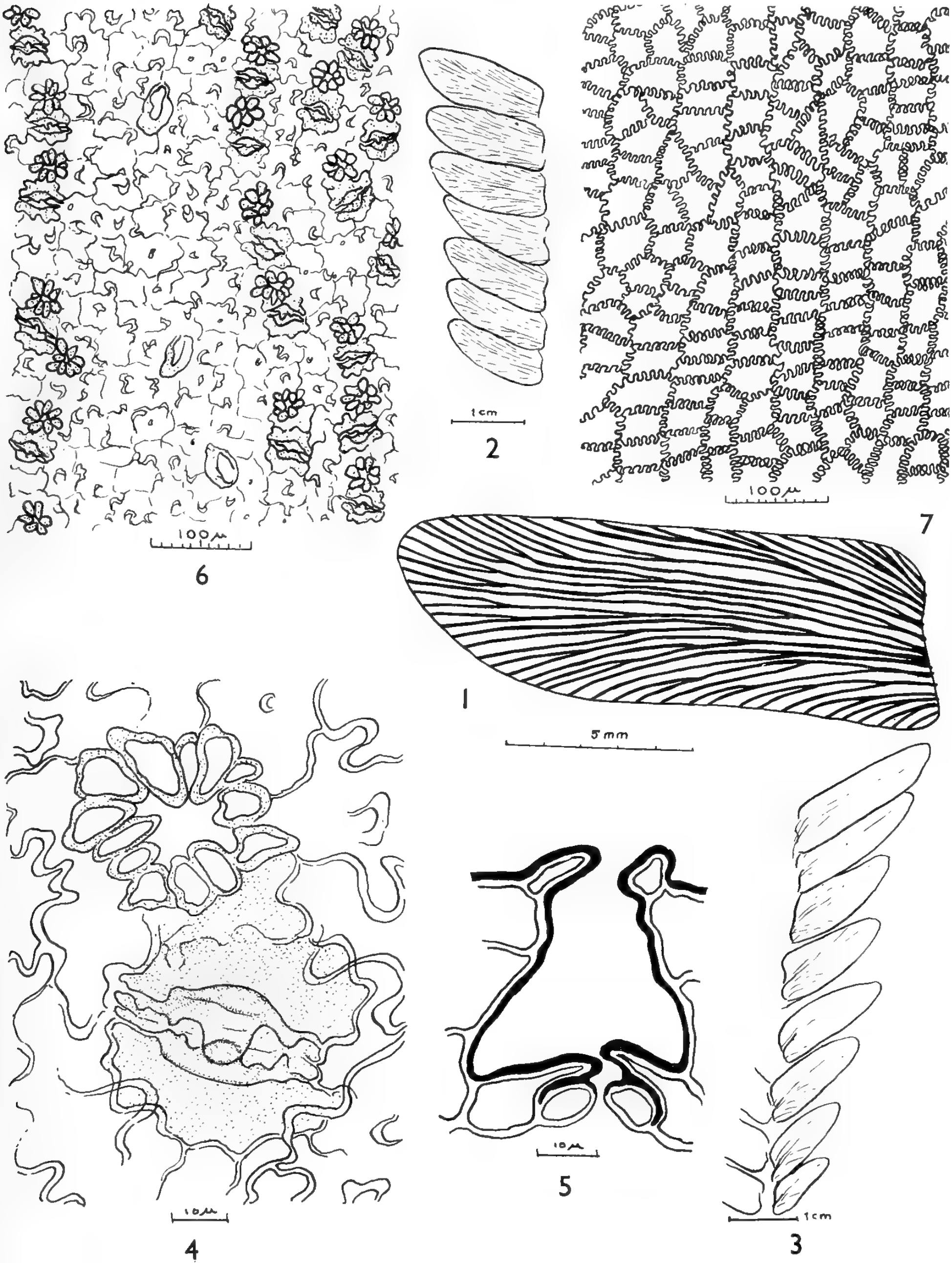
Upper cuticle showing nearly uniform cells in more or less definite longitudinal rows, cells short, anticlinal walls well marked, strongly sinuous, interior of cell flat. Stomata and trichomes absent. Lower cuticle showing stomata in bands between veins. Epidermal cells both along and also between veins tending to be short and rectangular ; anticlinal walls rather finely marked or indistinct, coarsely and irregularly sinuous, much less sinuous than on upper side.

Epidermal cells both along veins and between veins bearing on their surfaces one or more papillae ; papillae not median in position ; hollow and appearing as a ring. Trichome bases consisting of one or two cells with a thickened surface and a large ring-shaped scar occasional along the veins.

Stomata orientated transversely to veins ; irregularly spaced but often forming longitudinal files. Guard cells sunken in a rectangular chamber, mouth of chamber not placed over guard cells ; strongly constricted by a rosette of about twelve small papillae. Guard cells well cutinized ; subsidiary cells extending well beyond guard cells, each bearing a papilla over aperture of guard cells.

HOLOTYPE. LIL no. 2600 (Instituto Miguel Lillo, Tucuman).

FIGS. 1–7. *Otozamites parviauriculata* sp. nov. Fig. 1. Details of nervation of pinnae. LIL 2600. Figs. 2, 3. Diagrams showing the form of the pinnae. LIL 2600 and V.45372. Fig. 4. Stoma sunken in the bottom of the outer stomatal chamber with its aperture encircled by a crown of papillose cells. LIL 2600. Fig. 5. Section of stoma. Fig. 6. Lower epidermis with stomata aligned in spaces between nerves, hairs and numerous papillae. LIL 2600. Fig. 7. Upper epidermis. LIL 2600.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Other material. British Museum (Nat. Hist.) No. V.45372 ; BAPB nos. 7661, 7909, 7963 (Mus. Argent. Cienc. Nat. Palaeobot.).

Description. All the specimens are figured and all have very similar cuticles except that in Pl. 1, fig. 2 which has rather longer cells and the specimen in Text-fig. 3 which is preserved in a coarse sandstone just above the others and has no cuticle. At the pinna margins the epidermal cells become more elongated.

Comparison. Rather similar stomata are known in other species of *Otozamites* for example *O. pterophylloides* (Florin 1931), *O. beani* and *O. graphicus* (Harris 1944, 1950), but in none of these is the rosette round the aperture of the pit so well marked, nor do the subsidiary cells bear conspicuous papillae. The pinnae in these three European species are of different shape and have better developed auricles.

Of comparable specimens from S. America ; *O. genuensis* Feruglio (1934) from the Lias of Rio Genua, Chubut (which is based on a single fragment of unknown structure) has rather broader pinnae. The specimens determined as *O. obtusus* L. & H. by Ferello (1947) have pinnae of similar size but larger auricles and more divergent veins. *O. obtusus* L. & H. (=*O. bechei*) from the type locality (see Harris 1961) differs both in shape of the pinnae and in cuticle. The specimens from Mexico determined by Wieland (1914) as *O. reglei* var. *luccrensis* are larger with more widely spaced veins.

Otozamites grandis sp. nov.

(Pl. 1, figs. 4–6, Pl. 2, figs. 9, 10 ; Text-figs. 8–12)

Diagnosis. Leaf up to 12 cm. wide. Pinnae coriaceous, from 23 mm. × 9 mm. to 60 mm. × 20 mm., arising almost at right angles to the rachis, contiguous or slightly overlapping, margins nearly parallel, apex obtuse, very slightly curved forwards. Pinnae attached to upper surface of rachis but leaving much of this surface exposed, region of attachment middle third of the pinna base. Auricle only very slightly developed, basal angle rounded. Veins radiating almost symmetrically, forking to maintain a concentration of about 20 per cm. Upper cuticle almost uniform. Cells rectangular or of irregular shapes, anticlinal walls strongly marked, rather closely sinuous, leaving much of cell surface unmarked and flat. Lower cuticle thinner, anticlinal walls of cells less clearly marked, only slightly and irregularly sinuous except near pinna margins.

Cells along veins bearing clusters of hollow papillae or a large compound papillae, cells between veins bearing a small papilla cluster or single hollow papillae or with none.

Figs. 8–12. *Otozamites grandis* sp. nov. Fig. 8. Details of nervation of pinnae. Fig. 9. Upper epidermis. B.M. (N.H.), V.45370. Fig. 10. Lower epidermis showing stomata in longitudinal rows, papillose trichomes and papillae. V.45370. Fig. 11. Clustered papillose trichomes. V.45370. Fig. 12. Stoma and papillae. V.45370.

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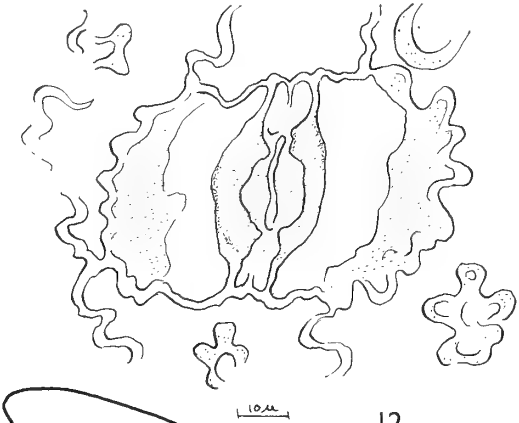

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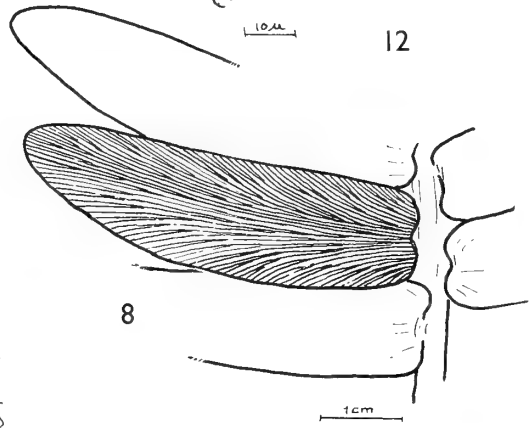

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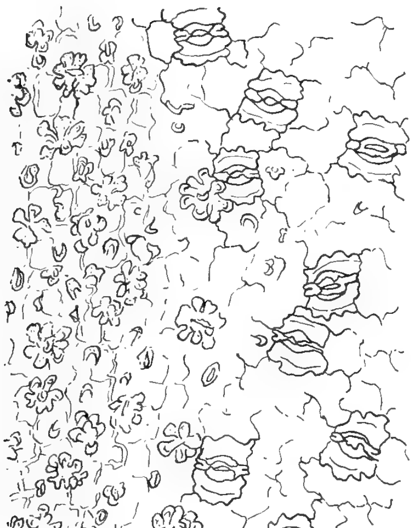

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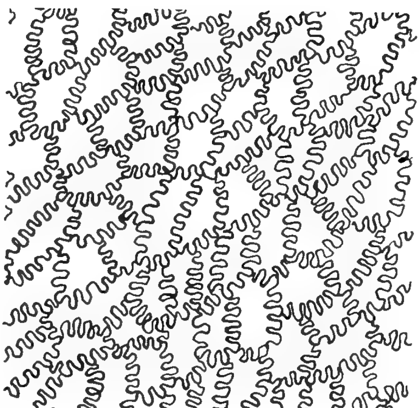

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Stomata occurring in broad bands between veins, occasionally along veins, transversely orientated but irregularly spaced and not forming files. Guard cells level with epidermal surface thickly cutinized. Subsidiary cells rather broad, outer anticlinal walls very broad and prominent.

HOLOTYPE. LIL no. 2590.

OTHER MATERIAL. In addition to the holotype, BAPB 7964–65, 7967–69; Brit. Mus. (Nat. Hist.) nos. V.45370–71; LPPB 5900 (Mus. Cienc. Nat. La Plata).

DESCRIPTION. There are a few specimens in addition to those figured; of those which are not illustrated LPPB 5900 has pinnae 5 cm. × 1·3 cm. and is like the holotype except that the pinnae have slightly more acute apices. Specimen BAPB 7966, with pinnae measuring 5·5 cm. × 1·5 cm., shows the whole width of the rachis (5·5 mm.). Its surface shows longitudinal striae and irregular furrows. BAPB 7967 has the smallest pinnae (2·3 × 0·9 cm.) and BAPB 7965 perhaps the largest, has a pinna fragment 2 cm. wide. The largest fragments are up to 15 cm. long and from the diminution of the size of the pinnae it is probable that the leaf was lanceolate and 30–45 cm. long.

DISCUSSION. *O. grandis* (like *O. parviauriculata*) is remarkable for the almost symmetrical attachment of the pinnae which thus approach the genus *Zamites*. The compound papillae are a remarkable feature of this species.

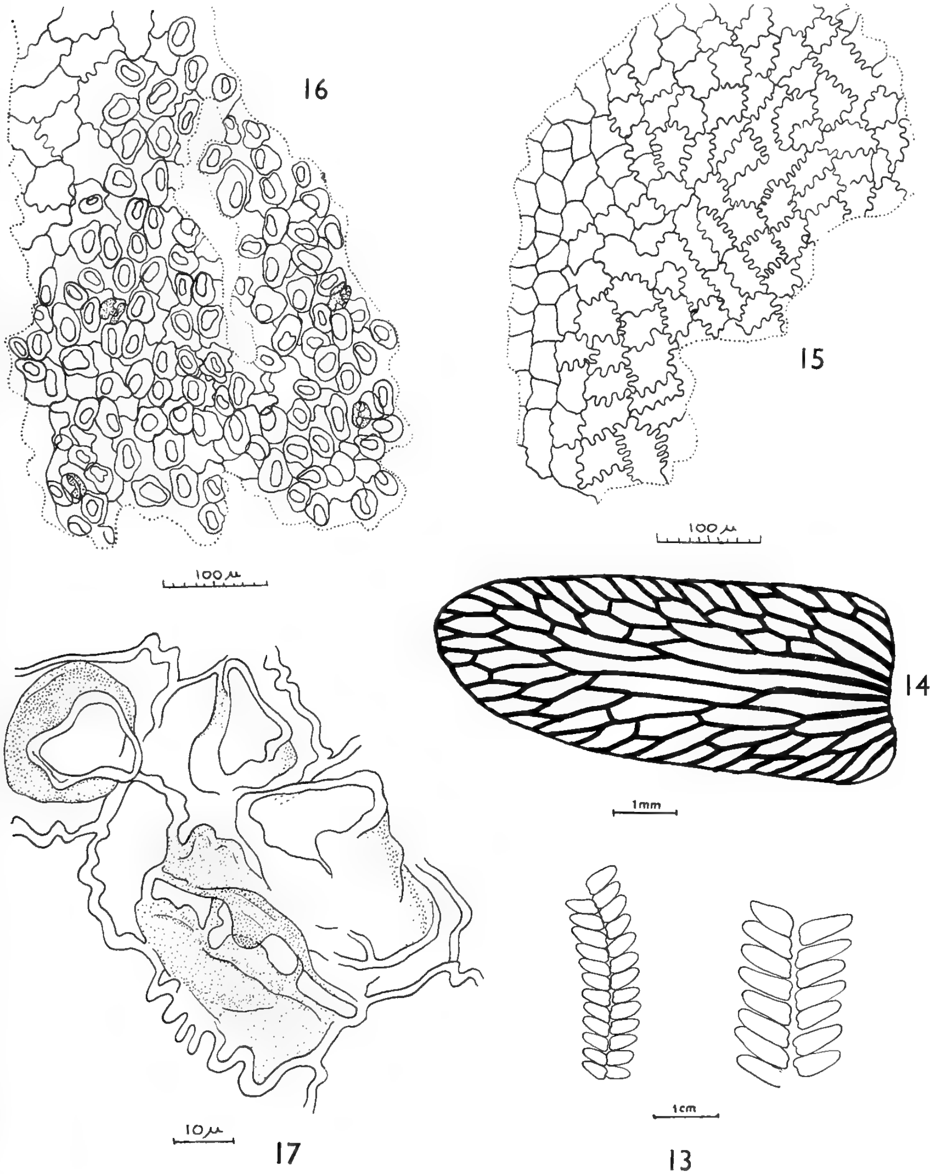
COMPARISON. No *Otozamites* (or *Zamites*) species is known with pinnae of this size, shape and cuticle. A few species of undescribed structure match *O. grandis* more or less in form. These include *O. giganteus* Thomas 1911 (Middle Jurassic of Kamenka, Russia). Unfortunately the pinna apex is not known so that even the gross features are imperfectly comparable. Specimens from the English Wealden determined by Seward (1895) as *O. klipsteinii* (Dunker) are similar but though the pinnae are as large, they are wider and more obtuse. Even Seward's *O. klipsteinii* var. *longifolius* has wider and more obtuse pinnae than *O. grandis*. *O. oaxacensis* Wieland (1914) from the Lias of Mexico has pinnae of similar size and general shape but with much more acute apices.

Genus ***DICTYOZAMITES*** (Oldham)

Dictyozamites minusculus sp. nov.

(Pl. 3; Text-figs. 13–17)

DIAGNOSIS. Leaf 1–3 cm. broad, lanceolate (?); pinnae up to 21 mm. × 3 mm.; smaller ones 5 mm. × 3 mm. Pinnae arising at an angle of 60°–90° to the rachis, typically just in contact. Margins straight and parallel for over half the length of the pinna, then converging equally to a rounded apex, or in largest pinnae apex obtuse; basal margin slightly retuse, attached almost symmetrically to upper surface of rachis in the middle third, both basal angles rounded; or in obliquely attached pinnae, upper angle reduced. Substance of pinna thick. Veins conspicuous, middle ones almost longitudinal but lateral ones diverging to meet the margins at an angle



FIGS. 13–17. *Dictyozamites minusculus* sp. nov. Fig. 13. Fragments of frond with long and small pinnae. BAPB 7971. Fig. 14. Details of pinna, showing nervation. BAPB 7976. Fig. 15. Upper epidermis showing cell walls becoming less sinuous towards basal part of pinna (left). LIL 2591. Fig. 16. Lower epidermis showing stomata, trichome bases and papillae. BAPB 7976. Fig. 17. Cuticle showing stoma with papillae on the aperture and trichome bases. BAPB 7976.

of about 35°, veins conspicuous, traversing the lamina at a concentration of about 20 per cm., anastomosing, median vein meshes several mm. long but marginal ones about 1 mm. long.

Upper cuticle showing cells with sinuous walls ; cells over veins and near margins elongated ; surface flat (with no papilla ; stomata and trichomes absent). Towards pinna base cells becoming straight walled. Lower cuticle showing cells with sinuous but inconspicuous anticlinal walls. Epidermal cells each bearing a hollow papilla on its surface ; smallest papillae one fifth of diameter of cell, larger ones occupying most of the surface ; free ends of papillae often expanded and overlapping their bases. Papillae less developed towards margins and base of pinna. Stomata scattered in areas between veins, transversely orientated (Pl. 3, fig. 14). Guard cells situated on the surface, well thickened, aperture protected by well developed solid papilla on each subsidiary cell. Subsidiary cells rather small, outer anticlinal walls broad and thick.

HOLOTYPE. LIL no. 2591.

OTHER MATERIAL. In addition to the holotype, Brit. Mus. (Nat. Hist.) nos. V.45374–75 ; BAPB nos. 7971–72, 7976 ; LPPB 5899.

DESCRIPTION. In addition to the figured specimens there are a number of detached pinnae (the smallest 3·5 × 2·5 mm.) and a few leaf fragments like those figured. Certain rather large specimens are probably of this species but being preserved in a coarse matrix in which fine details have been destroyed, their determination is less secure. In several specimens the cuticle was difficult to detach and prepare.

COMPARISON. The material is large enough to show a moderate range of form, mainly in the size of the pinnae and in the angle of their insertion. *D. minusculus* is distinguished from the Indian specimens of *D. falcatus* (also called *Dictyopteris falcata* var. *obtusa*) and *Dictyozamites indicus* see Oldham & Morris (1863), Feistmantel (1877*a*) by never having falcate pinnae. A specimen figured by Feistmantel (1878, pl. 3, fig. 3, 3*a*) is less different but most of the associated specimens are broader. It appears that in *D. minusculus* the pinnae are of constant width over the whole leaf, but in the Indian specimens the width varies with the position on the rachis. The specimens from Bahia Tekenika, Tierra del Fuego (Halle 1913) determined as *D.* cf. *falcatus* also have falcate pinnae. *D. hallei* Sahni & Rao (1936) and Jacob (1951) has even narrower pinnae, 12–15 mm. × 2 mm., and they are also falcate. *D. johnstrupi* (see Nathorst 1907) from the Jurassic of Bornholm has larger pinnae and *D. hawelli* (see Seward 1917) have larger pinnae and the cuticles are distinguished by the much smaller papillae on the lower side.

Dictyozamites crassinervis sp. nov.

(Pl. 4, fig. 16 ; Pl. 5, figs. 21, 22 ; Text-figs. 18–20)

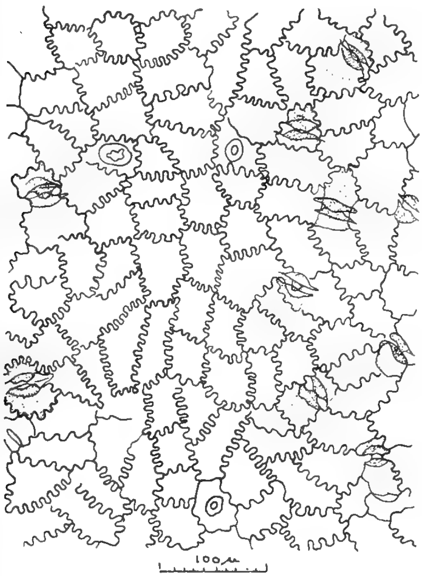
DIAGNOSIS. Leaf about 11 cm. wide. Pinnae arising at about 80°, almost in contact. Pinnae about 6 cm. × 2·5 cm., margins parallel over most of the pinna (apex not known), basal margin truncate, both basal angles rounded, similar or

lower one enlarged. Veins arising from a small part of middle of basal margin, thick, middle ones longitudinal and parallel but lateral ones curving out to meet the margins at an angle of about 45°. Veins traversing lamina at a concentration of 6–10 cm.; in middle of pinna meshes 1 cm. or more long but towards margins meshes reduced to 2–3 mm. Upper cuticle showing sinuous walled cells, somewhat elongated along veins, without papillae, stomata absent, a few trichome bases present. Lower cuticle divided into stomatal areas between veins and strips along veins with none. Cells along veins somewhat elongated longitudinally, cells between veins variable but often transversely elongated; anticlinal walls of all cells conspicuous, rather finely sinuous interiors of cells usually flat but a few cells showing a small solid papilla.

Stomata on surface, scattered in areas between veins mostly orientated transversely to veins. Guard cells well cutinized, subsidiary cells small, with thick outer walls usually with one or two papillae projecting over the aperture, but occasionally with no papillae. Trichome bases occasional on veins and among stomata, consisting of normal sized cell with thickened surface.

HOLOTYPE. BAPB no. 7979.

OTHER MATERIAL. In addition to the holotype, one specimen BAPB no. 7970.



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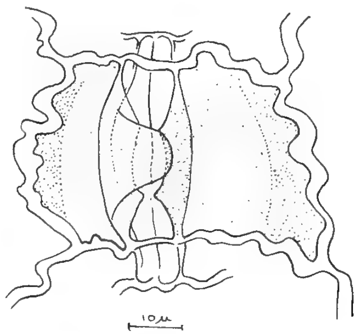

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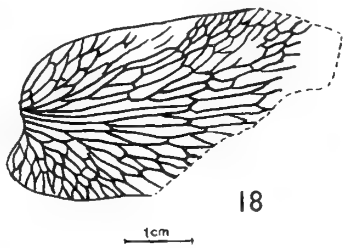

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FIGS. 18–20. *Dictyozamites crassinervis* sp. nov. Fig. 18. Fragment of pinna showing details of nervation. BAPB 7970. Fig. 19. Lower epidermis with stomata transversely arranged between nerves, sparse papillae and trichome bases. BAPB 7979. Fig. 20. Stoma from lower epidermis. BAPB 7979.

DESCRIPTION AND COMPARISON. *D. crassinervis* is only represented by the two figured specimens. Unfortunately the apices of the pinnae are missing in both. *D. crassinervis* is like *D. latifolius* in many respects but the veins are much coarser and the meshes much larger. The stomata of *D. crassinervis* sometimes lack papillae altogether, but those of *D. latifolius* are protected by at least two and often by three or four.

Dictyozamites latifolius sp. nov.

(Pl. 4, figs. 17–20; Pl. 5, figs. 23, 24; Text-figs. 21–24)

DIAGNOSIS. Leaf up to 13 cm. wide. Pinnae up to 6·5 cm. × 3 cm. but often somewhat smaller, shape almost oblong but widest near the base and lateral margins approaching gradually to near the apex and then contracting more rapidly to an obtuse point, acroscopic margin straight or slightly concave, basal margin truncate, attachment by a small area in the middle, basal angles rounded, basiscopic angle slightly expanded.

Pinnae diverging from rachis at an angle of 50°–90°, lateral margins typically in contact. Veins prominent, consisting of about 10 almost longitudinal ones along middle of pinna and lateral ones diverging from it to meet the margins at an angle of about 30°; concentration about 15 per cm., meshes in middle region 5 mm. or more long, but reduced to about 1 mm. or even less near margins, at basal angles lateral veins curving to run almost parallel with rachis.

Upper cuticle showing rather uniform, slightly elongated cells, anticlinal walls rather coarsely sinuous; surface flat. Stomata absent, trichome bases consisting of single oval cell bearing ring-shaped scar, occasional.

Lower cuticle showing slightly elongated cells along veins, cells between veins isodiametric or transversely elongated. Surface of most cells flat or very obscurely papillate. Anticlinal walls coarsely sinuous. Papillae normally absent. Stomata numerous confined to areas between veins, orientated transversely, rather evenly spaced. Guard cells strongly cutinized, subsidiary cells rather small, whole surface strongly cutinized and each subsidiary cell bearing a large hollow papilla pointing over the aperture. Adjacent epidermal cells often bearing hollow papillae pointing towards the aperture and often covering guard cell poles; occasional cells with similar papillae. Unicellular trichome bases scattered, as on upper side.

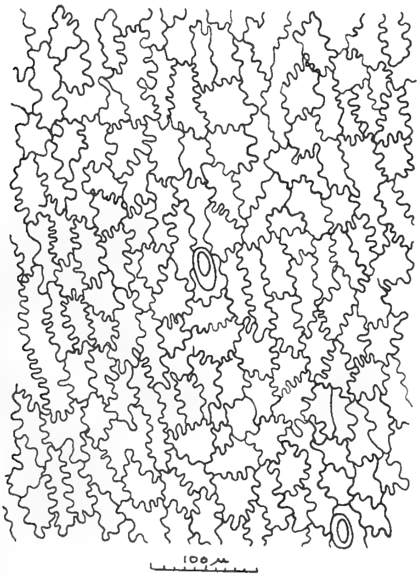
HOLOTYPE. BAPB no. 7995.

OTHER MATERIAL. In addition to the holotype, LIL no. 2597; Brit. Mus. (Nat. Hist.) no. V.45376; BAPB nos. 7916–17; LPPB no. 5894.

DESCRIPTION. There are five specimens besides the holotype and four are figured. The figured cuticles came from an isolated pinna, the largest specimen (Pl. 4, fig. 17) is preserved in a coarse sandstone and fine details are lost.

COMPARISON. *D. latifolius* somewhat resembles *D. hawelli* from the English Middle Jurassic, but its pinnae are larger and the lower angles more developed. The leaf determined as *D.* cf. *falcatus* by Halle from the Middle Jurassic of Bahia

Tekenika, Chile differs in its narrower pinnae and expanded upper basal angle which forms an auricle, while the lower one does not. A single fragment determined as *D. falcatus* by Cazaubon (1947) from the Upper Liassic of Esquel, Chubut has pinnae with a more acute apex and more widely spaced veins. The original Indian material of *D. falcatus* described by Oldham & Morris though varied shows more pointed and falcate pinnae.



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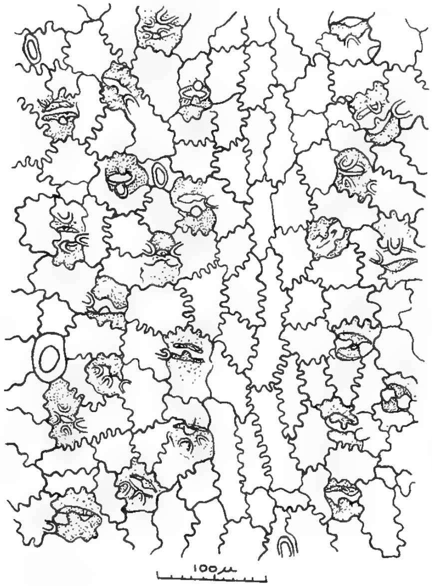

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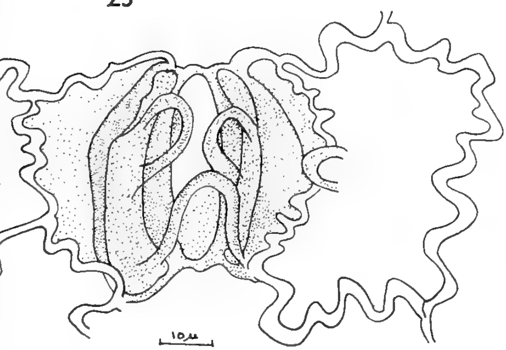

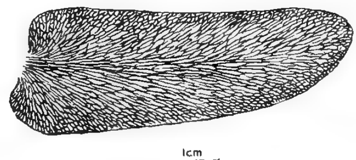

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FIGS. 21–24. *Dictyozamites latifolius* sp. nov. Fig. 21. Details of pinna, showing venation. BAPB 7917. Fig. 22. Lower epidermis, showing elongated cells on nerves and stomata between them. LIL 2597. Fig. 23. Upper epidermis. LIL 2597. Fig. 24. Stoma with papillae on the aperture. LIL 2597.

Genus ***PTILOPHYLLUM*** Morris

Ptilophyllum longipinnatum sp. nov.

(Pl. 6; Text-figs. 25–31)

DIAGNOSIS. Length of leaf exceeding 20 cm., width in middle region about 6 cm., apex rounded, base tapered. Typical pinnae straight, 3 cm. × 3 mm. or less to 4 cm. × 4·5 mm.; width uniform to near apex or width increasing slightly at first and then narrowing slightly. Pinnae separated by short intervals, attached at an angle of 45° to rachis; but at a smaller angle near leaf apex, apices of pinnae acute, bases truncate, basal angles rounded or rectangular, not expanded. Veins parallel, at a concentration of about 40–50 per cm.

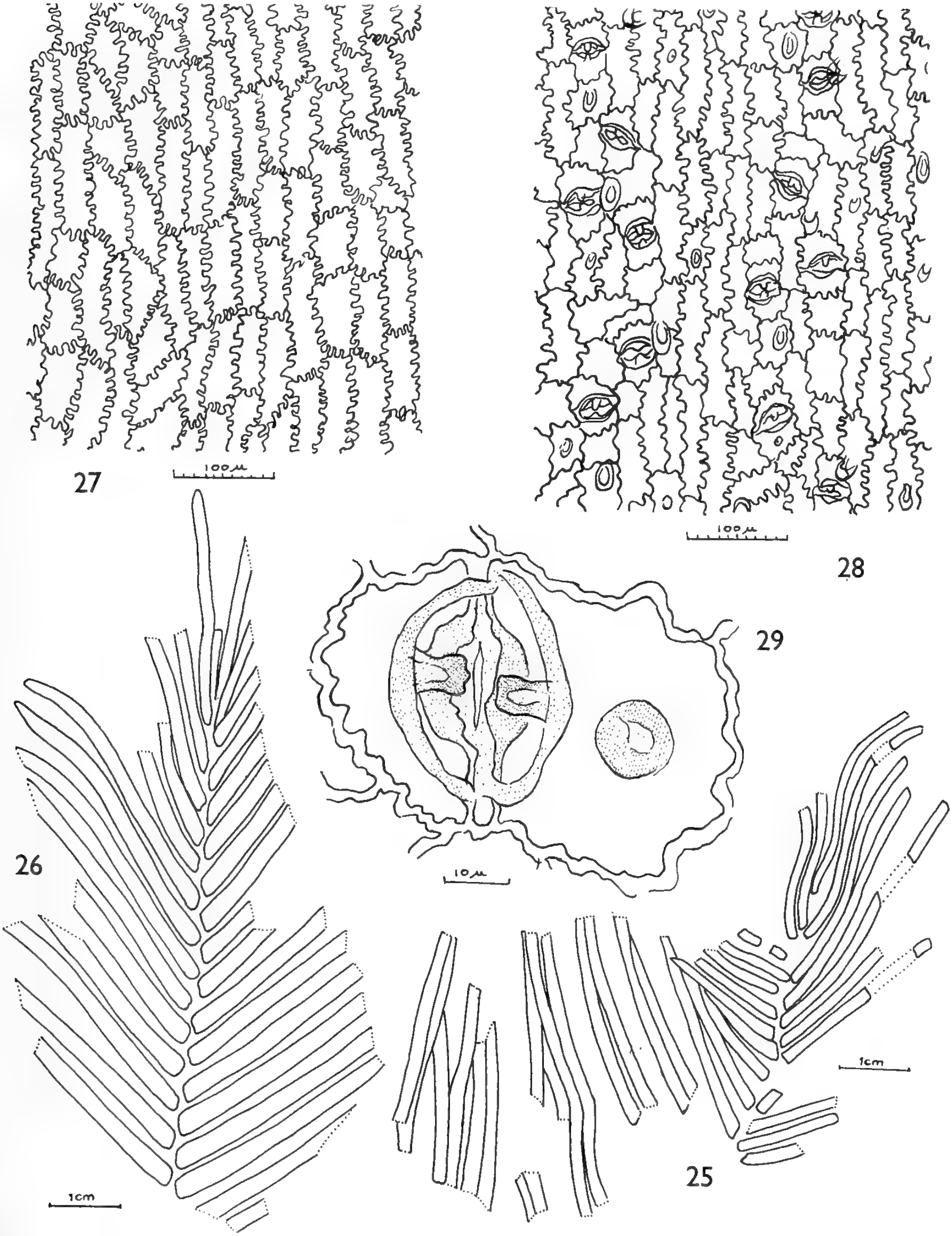
Upper cuticle showing somewhat elongated cells, narrower along veins, anticlinal walls coarsely sinuous, surface flat. Stomata and trichomes absent. Lower cuticle showing similar cells, but anticlinal walls less well marked. Stomata confined to strips between veins, forming about two indefinite files, orientated transversely but irregularly spaced. Ordinary epidermal cells often showing small or medium sized prominent hollow papilla; towards margins papillae and trichome bases often much more strongly developed, being present on nearly every cell, apices of papillae very thickly cutinized and often distinctly lobed. Guard cells slightly sunken, thickly cutinized, subsidiary cells small with strongly marked entire outer walls and prominent hollow papillae pointing over the aperture.

HOLOTYPE. BAPB no. 7940.

OTHER MATERIAL. In addition to the holotype, Brit. Mus. (Nat. Hist.) nos. V. 45377–78; BAPB nos. 7943, 7951, 7956–57; LIL no. 2595; LPPB no. 5898.

DESCRIPTION. *P. longipinnatum* is represented by several specimens besides the holotype. All have long, narrow pinnae, and the most complete, BAPB 7940 (holotype), is a fragment 20 cm. long with pinnae 2·5 cm. long below but increasing to 4 cm. and then decreasing to 3·3 cm., their width is 2·5 cm. throughout. The rachis which is largely concealed is about 2 mm. wide in the lower parts, 1 mm. above.

COMPARISON. *P. longipinnatum* is not a typical *Ptilophyllum*, and indeed it approaches *Zamites* in the sense in which Halle defined it. However its general characters are perhaps more like those of a *Ptilophyllum* than a *Zamites* and the pinna base is not at all constricted. It is distinguished from all described species of *Ptilophyllum* by its very long, narrow pinnae, as well as from most by the absence of a decurrent basal angle to the pinnae. Its cuticle is distinct; most of the lower surface is like that of *P. pectinoides* for example, but towards the margin the strongly developed papillae recall those of *P. hirsutum* (see Harris 1949). *Zamites proximus* Feistmantel (1877) from the Jurassic of India has rather similar pinnae but they are contracted at their bases.



FIGS. 25–29. *Ptilophyllum longipinnatum* sp. nov. Fig. 25. Terminal part of a frond. B.M. (N.H.), V.45377. Fig. 26. Fragment of the apical part of a frond. LIL 2595. Fig. 27. Upper epidermis. BAPB 7957. Fig. 28. Lower epidermis. BAPB 7957. Fig. 29. Stoma with papillae on the aperture and isolated papilla. BAPB 7940.

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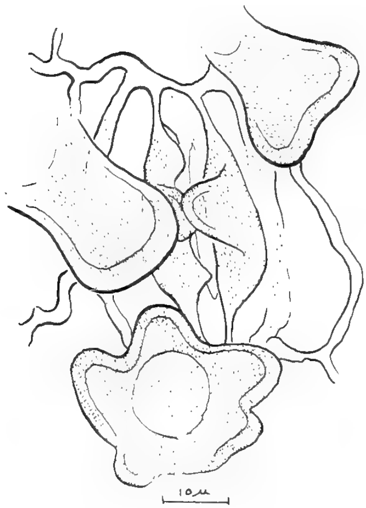

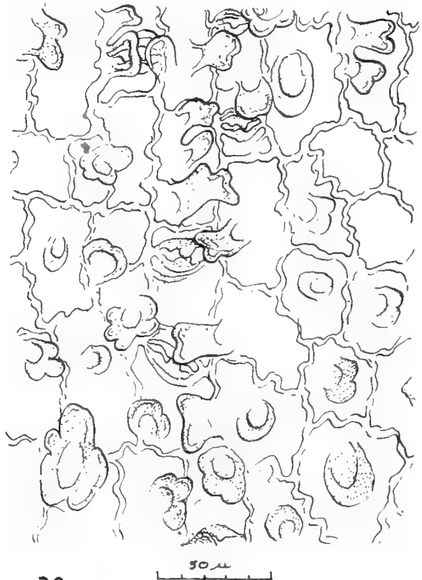

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FIGS. 30, 31. *Ptilophyllum longipinnatum* sp. nov. Fig. 30. Lower epidermis from margin of pinna with numerous large papillae. BAPB 7943. Fig. 31. Stoma surrounded by papillae. BAPB 7943.

Ptilophyllum hislopi (Oldham) Seward

(Pl. 7, fig. 29)

The material consists of a number of leaves preserved in a matrix in which the cuticle has been lost. Pl. 7, fig. 29 shows a typical specimen. Another specimen, BAPB 8004, which represents the lower part of the lamina shows pinnae 17 mm. × 4 mm. above decreasing to 14 mm. × 3 mm. below. The rachis is 3 mm. wide below. The veins are seen to be parallel and occasionally forked.

COMPARISON. Since this species is imperfectly known identification must be insecure. Similar leaves (also without microscopic details) have been described under this name from the S. American region. Halle (1913) figured very similar leaves from the Middle Jurassic of Graham Land, and Menéndez (1956) figured another from the Middle Jurassic of Neuquen.

Less similar are the leaves figured as *P. hislopi* by Frenguelli (1935) from the Upper Jurassic of Santa Cruz which have more rigid and acute pinnae. The Ticó specimens agree well in shape with the Indian originals but we have of course no details to compare.

Genus *PTEROPHYLLUM* Brongniart

Pterophyllum sp.

(Pl. 7, figs. 30–32 ; Text-figs. 32–34)

Description. The most complete specimen is shown in Pl. 7, fig. 30, unfortunately the apices of the pinnae are missing. The pinnae are attached to the thin rachis by their whole bases. The veins are conspicuous, they fork occasionally and there are 12–14 veins in each pinna. Another specimen, BAPB 7980, shows pinnae 3 cm. long and tapering from 4 mm. at the base to 2 mm. wide towards the free end.

Only the lower cuticle is preserved, its characters are clearly seen in Pl. 7, fig. 31 ; Text-fig. 33. Very small papillae are discernible above the guard cell thickenings in Pl. 7, fig. 32.

Comparison. No very similar leaf has been described from Argentina. The leaf determined as *P. rajmahalense* by Kurtz (1921) from Rio Atuel has longer pinnae ; *P. barrealense* Frenguelli (1950) from the Trias of Barreal, San Juan has more widely separated pinnae and *Pterophyllum* sp. Kurtz (1921) from the Trias of Cacheuta, Mendoza has pinnae with more crowded veins and also a broader rachis.

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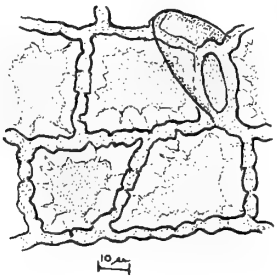

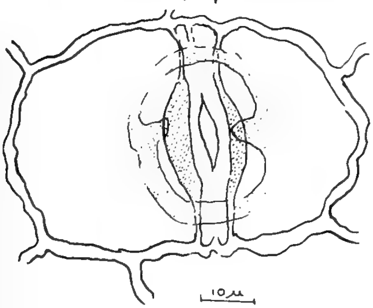

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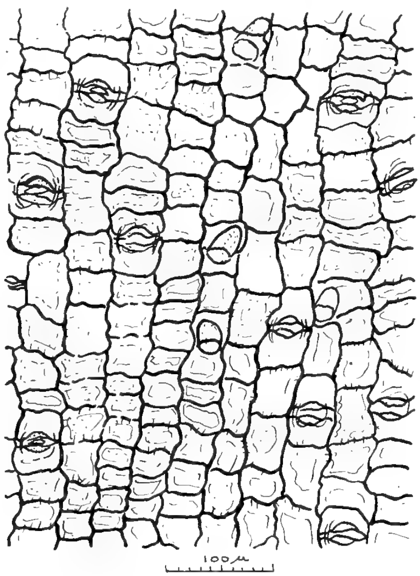

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Figs. 32–34. *Pterophyllum* sp. Fig. 32. Lower epidermis showing transversely orientated stomata, short hairs and cells with thickened surfaces. BAPB 7959. Fig. 33. Details of thickening of surface of cells and a short hair. BAPB 7959. Fig. 34. Stoma showing the thickening of the subsidiary cells and small papillae on both sides of the aperture. BAPB 7959.

The Ticó specimens are not well enough characterized to be worth comparing with leaves from more distant areas.

Genus *ZAMITES* Brongniart

Zamites decurrens sp. nov.

(Pls. 8, 9; Text-figs. 35–39)

DIAGNOSIS. Leaf large, rachis up to 8 mm. wide, bearing pinnae laterally, pinnae well spaced. Width of lamina 4–20 cm. Pinnae up to 9 cm. × 8 mm., but in smaller leaves 5·5 cm. × 4 mm. and 2 cm. × 3·2 mm. Pinnae almost straight; in large pinnae width increasing rapidly from near the base, then parallel then tapering to a rather acute apex. In smallest pinnae width increasing to near the rounded apex and shape thus spatulate. Basal angle always decurrent. Veins nearly parallel, fairly thick, forking occasionally at various levels.

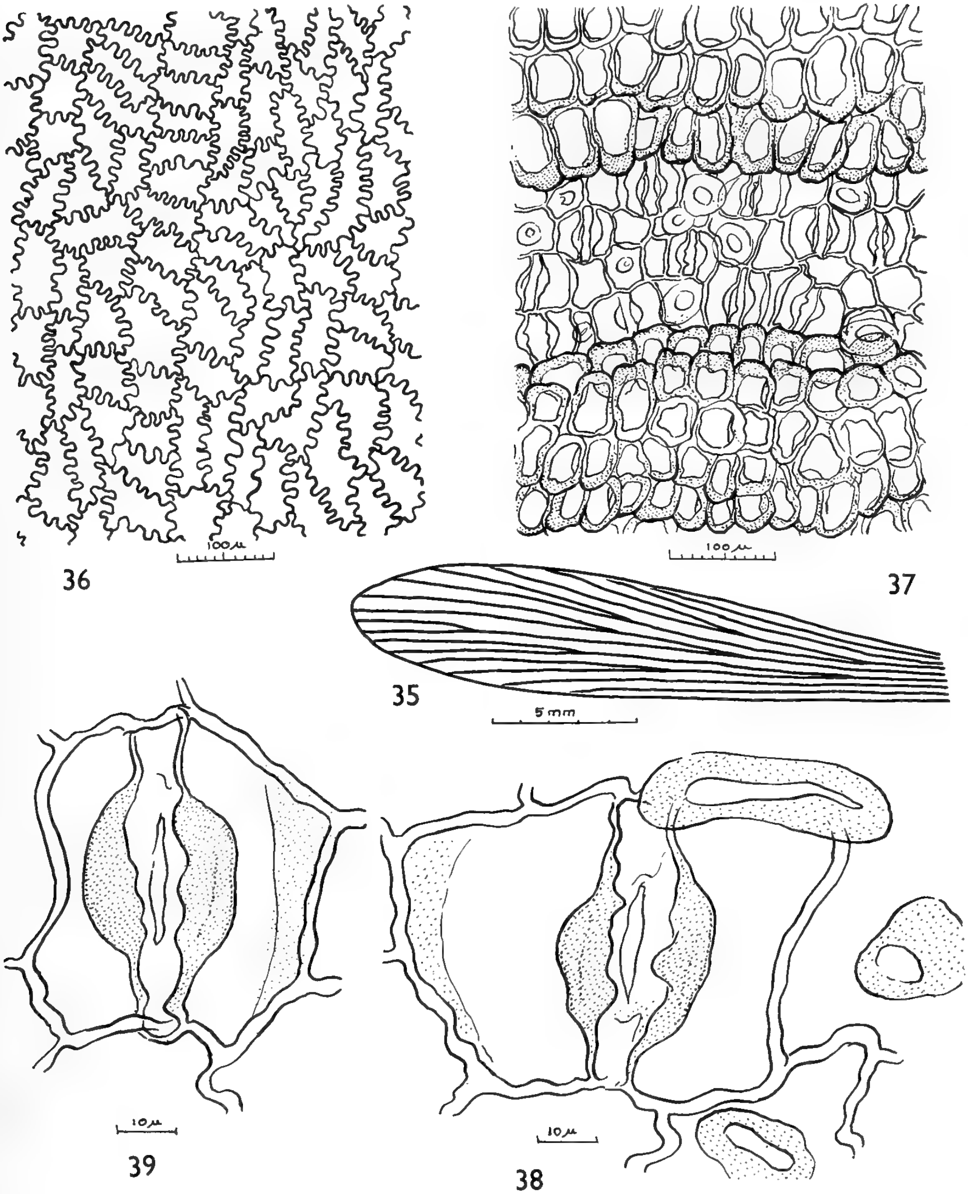
Upper cuticle showing nearly uniform, slightly elongated cells with strongly sinuous lateral walls. Stomata and trichomes absent. Lower cuticle showing folds along the sides of the raised veins. Cells along veins isodiametric, bulging in a globe and appearing thick-walled on compression; forming well marked longitudinal rows; trichome bases infrequent. Intervenal areas showing their true walls, approximately square, anticlinal walls straight, surface often occupied by a papilla, papillae hollow, sometimes small but often so large as to occupy the whole surface. Stomata transversely orientated, very numerous, forming well marked longitudinal files, but not quite evenly spaced in the files. Guard cells well thickened, subsidiary cells often as large as ordinary epidermal cells.

HOLOTYPE. LIL no. 2596.

OTHER MATERIAL. In addition to the holotype, Brit. Mus. (Nat. Hist.) nos. V.45379–80; BAPB nos. 7927–28; LPPB nos. 5888–89.

DESCRIPTION. The different specimens figured show a remarkable range both in the width of the leaf and in the form of the pinnae, but their very characteristic cuticles are just the same and for this reason they are included in the one species. In every one the lower basal angle of the pinnae is decurrent on to the rachis. The veins are almost parallel and some of the lateral ones end in the margins; this is most marked in the short pinna shown in Text-fig. 35. The specimen shown in Pl. 8, fig. 34 gives some indication of the length of the rachis, for it tapers in this fragment from 4 mm. to 2·4 mm.

COMPARISON. *Zamites buchianus* (Ett) from the English Wealden, see Seward (1895) is similar to some forms of *Z. decurrens* but it has longer pinnae. *Z. carruthersi* in the same flora has even larger pinnae. *Z. proximus* Feistmantel (1877) from the Indian Jurassic has narrower and less decurrent pinnae. In *Z. gigas* the pinnae differ in being attached to the top of the rachis. The cells along the veins do not form bulging gloves as in *Z. decurrens*.



FIGS. 35–39. *Zamites decurrens* sp. nov. Fig. 35. Details of nervation of pinna. BAPB 7927. Fig. 36. Upper epidermis. BAPB 7927. Fig. 37. Lower epidermis showing globose cells on the nerves and stomata, hairs and papillae between the nerves. BAPB 7927. Figs. 38, 39. Stomata and papillae on the lower epidermis.

Genus *WILLIAMSONIA* Carruthers

Williamsonia bulbiformis sp. nov.

(Pls. 10, 11 ; Text-figs. 40–53)

DIAGNOSIS. Female 'flower' with (10 to 14?) ribbon-shaped bracts, apices acute, thick, parallel nerved ; adaxial epidermis with thick cuticle, lacking stomata, cells aligned longitudinally, walls straight, cells rectangular, square or polygonal, elongated ; abaxial epidermis with thick cuticle and stomata, cells aligned longitudinally, walls straight, cells rectangular, square or polygonal, shorter than those of the adaxial epidermis ; outer, lateral and sometimes inner walls cutinized, hypodermis present ; epidermal hairs isolated and clustered in more or less transverse rows ; stomata scarce, transversely orientated, 10–14 per sq. mm., syndetocheilic. Guard cells with cutinized walls, subsidiary cells large. Fertile and sterile megasporophylls (interseminal scales) grouped in flattened pyriform cone (gynaecium) ; interseminal scales 4 to 7 mm. long, 1 mm. broad, and 14 mm. long and 3 mm. broad in mature specimens, polygonal in section and in juxtaposition, with apical part convex and well cutinized with a central dome, circular or polygonal in cross-section, 5 or 6 interseminal scales surrounding the fertile megasporophylls which project in surface a micropylar tube. Cells at apical part of interseminal scales straight and thick walled, concentrically arranged, central ones somewhat papillose and the walls thicker than those of marginal zone. Stomata scarce (2–6 per shield), concentrically arranged, generally with their main axis tangential, more rarely radial ; syndetocheilic with heavily cutinized guard cells, sunken, sometimes with papilla on the aperture. Micropylar tubes cylindric, broadening at base with cells longitudinally aligned, rectangular, square or trapezoidal, walls bulging and giving rise to the papillose surface of micropylar tube.

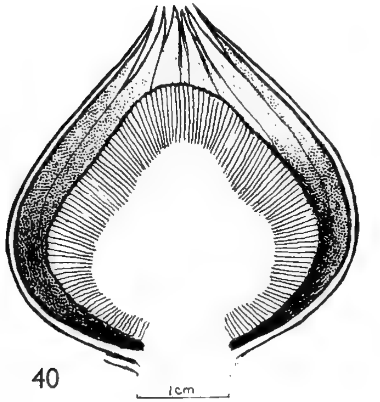
HOLOTYPE. LIL no. 2599.

OTHER MATERIAL. In addition to the holotype, BAPB nos. 7998–8000 ; Brit. Mus. (Nat. Hist.) nos. V.45381–82 ; LPPB nos. 5896–97.

DESCRIPTION. The most complete specimen is BAPB no. 7998. It has been compressed along its vertical axis which has resulted in the 'flowei' having a flattened conical shape, with the apex of the bracts displaced to one side (Pl. 10, figs. 39, 40). The hollow left by the receptacle is pyriform and flattened principally at the base with a maximum breadth of 3 mm. It is surrounded by the interseminal scales which are up to 7 mm. in length.

The bracts have a maximum width of 9–11 mm. at the basal region, decreasing gradually in width towards the apex. The basal part of the specimen is missing so that the length of the bracts can only be estimated as 6 to 7 cm. Some of the bracts were lost through breakage but the number present in the entire specimen was

FIGS. 40–48. *Williamsonia bulbiformis* sp. nov. Fig. 40. Reconstructed section of specimen BAPB 7998. Fig. 41. Reconstruction of general aspect of the 'flower'. Fig. 42. Schematic profile of specimen BAPB 7998. Fig. 43. Reconstructed section of specimen B.M. (N.H.) V.45381. Fig. 44. Reconstructed profile of specimen B.M.



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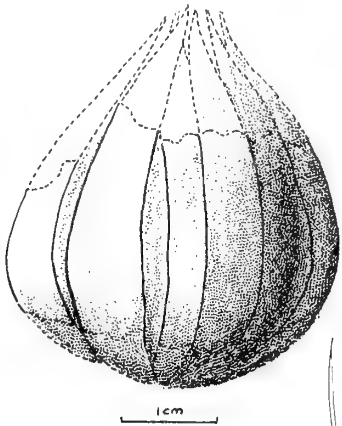

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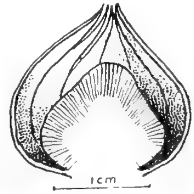

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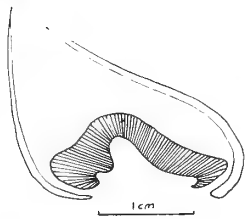

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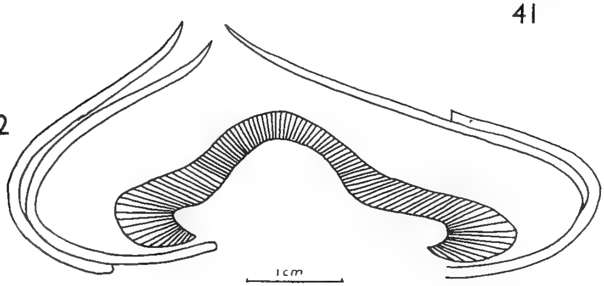

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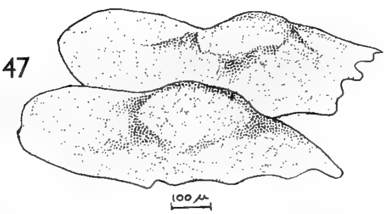

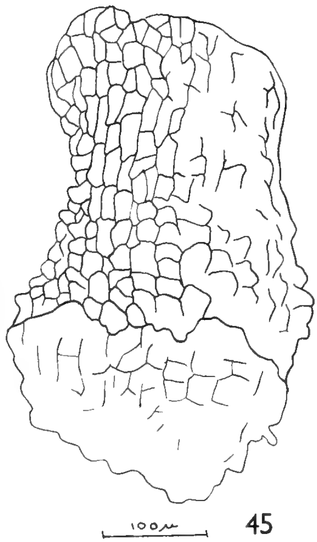

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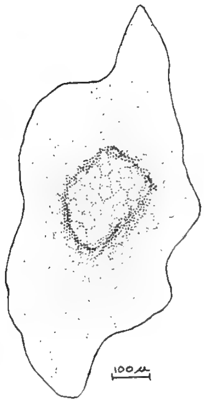

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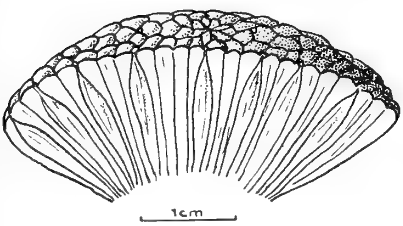

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(N.H.), V.45381. Fig. 45. Micropylar tube. BAPB 7999. Fig. 46. Apical part of interseminal scale with polygonal umbo. BAPB 7999. Fig. 47. Apical shields of interseminal scales in lateral view, showing the central dome or umbo. BAPB 7999. Fig. 48. Reconstructed section of specimen BAPB 7999.

probably 13–14. Of the 8 remaining, some of them overlap as if there was more than one series probably in helicoidal arrangement.

A diagrammatic reconstruction of this specimen is given in Text-figs. 40 and 42.

The holotype (Pl. 11, fig. 45) is the basal part of a 'flower', the circular area at the centre, which corresponds to the impression of the receptacle, is concave, slightly conical, 18 mm. in diameter, and is dense and finely pitted due to scars of the vascular bundles of the fertile and sterile megasporophylls (interseminal scales). Surrounding the receptacle in a ring are the lateral megasporophylls and interseminal scales in the form of striated tubes, 5 mm. long and 0·5 mm. wide, which appear to be formed from interseminal scales. Covering this ring-shaped zone of the megasporophylls were the bracts that wrap round the 'flower', which, after falling exposed the megasporophylls. On the inner part of the overlapping bracts is engraved the surface of the cone which forms the junction of fertile megasporophylls and interseminal scales. The close arrangement of the latter gives the surface the appearance of a net with polygonal mesh.

Parts of the interseminal scales are frequently found perfectly preserved and in some cases the micropylar tube is also present.

Of the bracts that surrounded and covered the 'flower' only fragments, approximately 5 mm. broad, remain, therefore if in its insertion in the receptacle there was no superposition, there should be a minimum number of from 10 to 11. The bracts are consistent because the organic matter preserved is generally thick but the venation is only faintly visible on the impression because it is embedded in the parenchyma. The faint longitudinal furrows that can be seen in the impressions correspond to the parallel nerves.

Specimen B.M. (N.H.) no. V.45381 (Pl. 10, fig. 41) is a 'flower' in which the impression of the receptacle is finely pitted, the encircling megasporophylls are 4 mm. long. The bracts that surround the 'flower' are from a sector corresponding approximately to one half of the 'flower' and are from 4·5 to 5·5 mm. wide. The most complete fragment of bract is 2·5 cm. long and decreases in width towards the apex, its total length was probably about 3 cm. In this specimen, in spite of the deformation due to compaction, the hollow corresponding to the receptacle has retained an approximately conical shape but with its lateral margins flattened. A diagrammatic reconstruction of the complete 'flower' is shown in Text-figs. 43 and 44.

Specimen B.M. (N.H.) no. V.45382 is the external mould of an aggregate of bracts which shows the ovoid shape characteristic of the closed 'flower' and this specimen was used to make the reconstruction in Text-fig. 41.

Fructification. Specimen BAPB 7999 (Pl. 10, fig. 42; Text-fig. 48) shows an interesting form of preservation; it is a fragment of a laterally cleaved fructification through a tangential plane and is without bracts. Only the external mould remains of the upper part of the fructification and this is 4·2 cm. in diameter. It bears traces of the cuticle from the outer surface of the sterile and fertile megasporophylls. Casts of the megasporophylls and of the interseminal scales continue under the mould as a result of infiltration of sediment into the tissues. The casts of the fertile megasporophylls are fusiform, longitudinally faceted, with acute apices elongated towards

the external mould at the surface where they correspond to the micropylar tubes. The length of the megasporophylls is 14 mm. and the width 3 mm. in its widest part. This is much larger than the megasporophylls in specimen LIL 2599 which are 5 mm. long and 1 mm. wide and even taking into account that these latter measurements correspond to marginal megasporophylls the size variation is quite striking. One possible explanation is that the larger specimen is a fertilized ' flower ' with developing seeds.

This specimen is included in *Williamsonia bulbiformis* in spite of the considerable difference in size of the interseminal scales, because the cuticle of the upper part of the scale is the same as that of the immature specimens described above.

Cuticle. Cuticles from the apical parts of the interseminal scales are perfectly preserved, but those from the remaining part of the scale which continue below the surface have been found in only one case, and in this region the shape of the interseminal scales is prismatic as a result of close contact between the scales. The cuticle forming the shield at the apex of the interseminal scales usually separates when treated with Schulze's solution, although it sometimes remains united. The shields are polygonal in outline and hemispherical in surface with a central dome or bulge circular in cross section (Text-figs. 46, 47). The straight and thick-walled cells are arranged concentrically around the centre of the shield (Pl. 10, fig. 44; Text-fig. 49). In some the main axis of the cells is orientated radially and in others tangentially, but there are also isodiametric cells. The cells are from 20 to 60 μ in length by 15 to 30 μ in width. At the centre they are somewhat papillose and the cell walls thicker than those of the marginal zone.

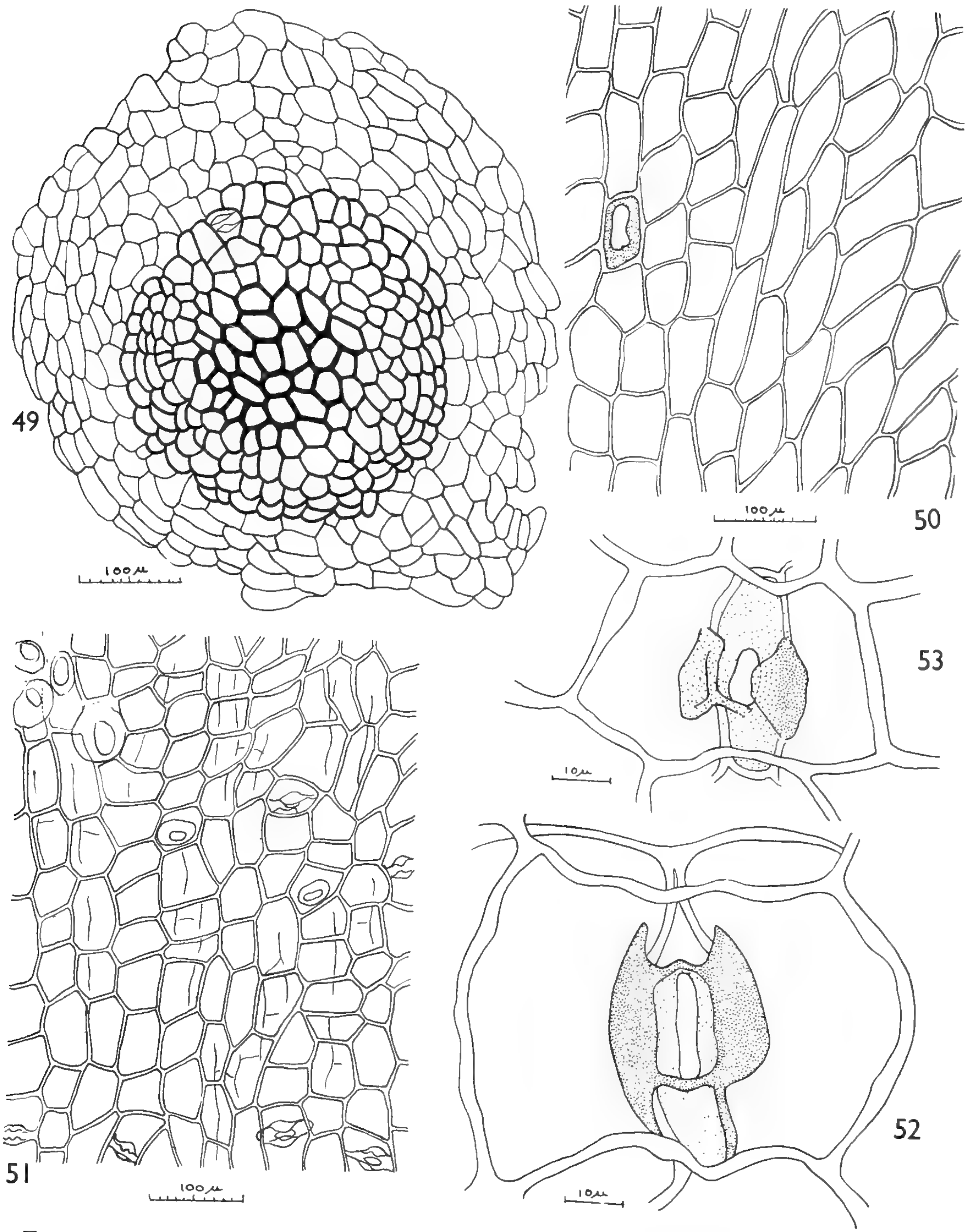
The shields possess from 2 to 6 stomata concentrically arranged both in the elevated zone at the centre and in the encircling zone although more frequently in the latter. The stomata are arranged with their longitudinal axes in a tangential direction or more rarely in a radial direction. They are syndetocheilic and sunken. The walls of the guard cells are heavily cutinized and even thicker than the lateral walls that abut with the subsidiary cells. One stoma was observed in which one papilla projected from a subsidiary cell towards the aperture. The stomata measure between 35 and 45 μ in length.

Five or six interseminal scales surround the fertile megasporophylls and from these, as noted above, the cuticle of the apical part encircling the micropylar tube was obtained.

The arrangement of these parts was only seen in the material before treatment with Schulze's solution, because after oxidation the scales and micropylar tube usually separate.

Only three micropylar tubes were obtained, all from specimen BAPB 7999, and although more than a score of preparations were made from other specimens micropylar tubes were not found. This indicates that the fertile megasporophylls do not occur at random among the interseminal scales but are confined to certain regions.

The micropylar tube (Text-fig. 45) is cylindrical, broader at the base than at the upper end, has a length of 300 μ, a breadth of 280 μ at the base, 200 μ at the narrowest part and 240 μ at the apical end. The cells are longitudinally aligned, rectangular,



Figs. 49–53. *Williamsonia bulbiformis* sp. nov. Fig. 49. Cuticle of the apical part of the interseminal scale (shield). LIL 2599. Fig. 50. Adaxial epidermis of a bract. LIL 2599. Fig. 51. Abaxial epidermis of a bract with stomata, hair bases and remains of hypodermis. LIL 2599. Figs. 52, 53. Stomata of abaxial epidermis of bract. LIL 2599.

square or trapezoidal with convex superficial walls which give rise to the papillose surface of the micropylar tube. The micropylar tube (Pl. 10, fig. 43) measures 300 μ in length and 222 μ, 175 μ and 225 μ respectively in basal, minimum and apical breadth.

Cuticle of bracts. The abaxial epidermis (Pl. 11, fig. 47 ; Text-fig. 51) of the bracts is different from the adaxial. The position of each of the cuticles was noted whilst they were still in the matrix, they were then removed and treated with Schulze's solution. In this way it was possible to show that only the abaxial epidermis possesses stomata.

The abaxial cuticle is thicker than the adaxial. It consists of cells aligned along the length of the bract, polygonal, elongated, rectangular or square and measuring 30 to 95 μ in length and 30 to 55 μ in width. Some of the rows of cells have longer cells than others.

The cuticle shows not only the outer walls of the cells but also the lateral walls, and in some parts the cuticle of the lower cell wall is preserved, where it replicates the outline of the cells of a hypodermis.

The stomata are orientated perpendicularly to the length of the bracts. They are like those of the interseminal scales, although the papillae of subsidiary cells are absent and the stomata are somewhat larger measuring 45 to 57 μ in length. In addition there are isolated hairs clustered in irregularly arranged transverse rows.

The adaxial epidermis (Pl. 11, fig. 46 ; Text-fig. 50) has cells of similar shape to those of the abaxial, although they are longer and the hypodermis is only weakly marked or entirely absent in some cuticles.

Discussion. The variations in size of *W. bulbiformis* are considered to be different stages of development of the 'flower' because in all of them the form and character of the anatomical structure of the preserved cuticle of the megasporophylls and bracts is alike. In specimen BAPB no. 7999 where the megasporophylls are larger than in the other specimens, their size is considered to be the result of subsequent development after fertilization to maturity.

Williamsonia blandfordi Feistmantel (1877 : 29, pl. 1, figs. 4, 5 ; pl. 2, fig. 6 ; 1880 : 52, pl. 12, figs. 5–7) from the Jurassic of India, greatly resembles *W. bulbiformis* in shape and size, but differs in the larger number of narrower bracts and in the smaller diameter of the receptacle.

Williamsonia carruthersi Seward (1895 : 157, pls. 10, 11 ; text-fig. 8) from the Wealden of England differs from *W. bulbiformis* in the greater width of the bracts and the relatively smaller size of the conical receptacle.

The smaller specimens of *Williamsonia gigas* (Williamson 1870 ; Feistmantel 1877) resemble *W. bulbiformis*, but the receptacle of the former is relatively longer and narrower, whilst the interseminal scales are also longer and possess bracts with marginal hairs.

Williamsonia leckenbyi Nathorst (1911 : 21, pl. 6, figs. 1–10 ; 1909 : 14, pl. 3, figs. 1–10) has a much smaller receptacle and the length of the megasporophylls is relatively greater.

Comparisons with other species of *Williamsonia* show even greater differences.

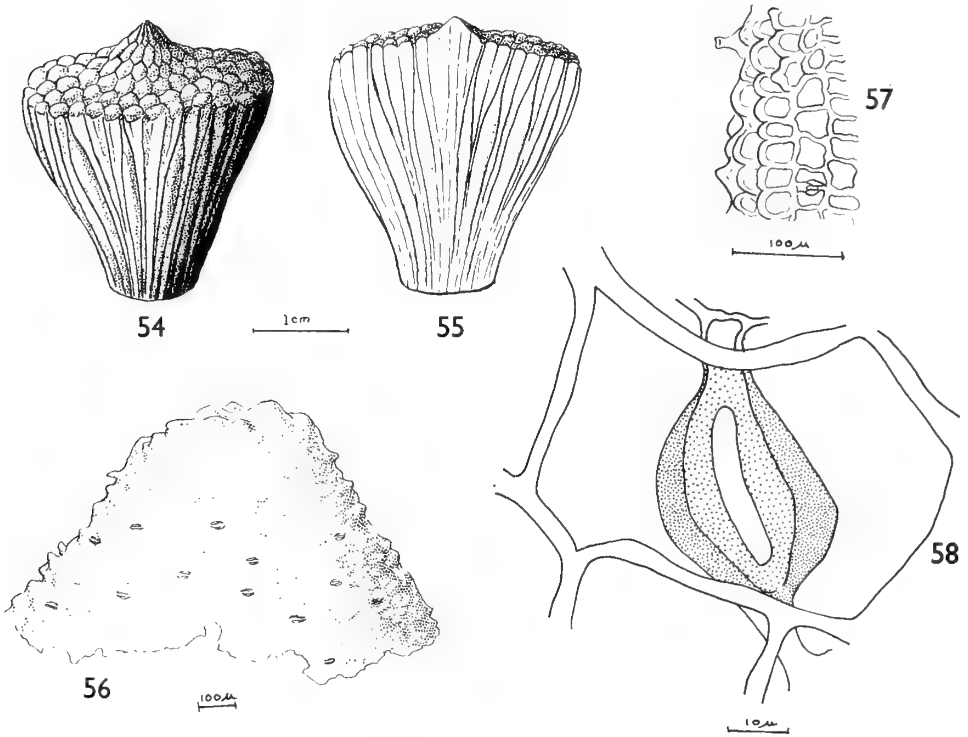
Williamsonia umbonata sp. nov.

(Pl. 12 ; Text-figs. 54–58)

Diagnosis. Female 'flower' (or fructification) umbonate, approximately 3 cm. in diameter, bracts not preserved, interseminal scales polygonal in outline, 5–6 sided, 1·5 to 2 mm. in diameter, encircling megasporophylls. Megasporophylls 26 mm. long, 3·5 mm. in maximum width, fusiform, ending in tube 2 mm. in length. Cuticle of shields of interseminal scales with thick-walled cells arranged concentrically, superficial wall deeply convex or forming papillae, some of which constitute hair bases. Stomata syndetocheilic, concentrically arranged, with guard cells sunken and lateral wall well cutinized.

Holotype. LIL no. 2598.

Other material. In addition to the holotype, BAPB no. 7997.



Figs. 54–58. *Williamsonia umbonata* sp. nov. Fig. 54. Reconstruction of possible shape of specimen BAPB 7997. Fig. 55. Reconstructed section of specimen BAPB 7997. Fig. 56. Apical part of interseminal scale showing papillose surface and distribution of stomata. BAPB 7997. Fig. 57. Details of cuticle of interseminal scale showing the papillose cells and hairs. BAPB 7997. Fig. 58. Stoma of interseminal scale. BAPB 7997.

Description. The holotype (Pl. 12, fig. 49) is the impression of the upper part of a female cone (gynaecium), 3 cm. in visible diameter, on which the extreme end of each of the interseminal scales has left a concavity, usually of polygonal contour, 5–6 sided, with diameters from 1·5 to 2 mm. In a few cases there is a radial arrangement of the interseminal scales around what should correspond to the micropylar tube of a fertile megasporophyll. In the majority of the concavities the cuticle of the interseminal scales is preserved.

In the middle of the specimen there is a funnel-shaped hollow which being an external mould probably represents an umbonate apex of the fructification or 'flower', in which the shields that form the apical part of the interseminal scales lengthen radially.

The size of the megasporophylls in specimen BAPB no. 7997 (Pl. 12, fig. 50; Text-figs. 54, 55) shows that it corresponds to a fructification, some megasporophylls of which have left their impression in the sediment and the greatest part having disappeared leaving a hollow. In the upper part of the hollow the cuticle of the apical shields of the megasporophylls still remains. This surface reproduces the original shape of the specimen, it is slightly hemispherical, 3 cm. in greatest diameter, with the central umbo equal to that in the holotype.

The sterile megasporophylls or interseminal scales are 26 mm. long, the fertile ones are fusiform and are 3·5 mm. wide tapering at the apex into a tube 2 mm. wide, corresponding to the micropylar tube. It is difficult to ascertain whether the organic remains of this specimen represent a complete fructification or only part of one. The position of the umbo in the centre and the equal size of both specimens suggest the approximate shape as in the reconstruction shown in Text-figs. 54 and 55.

Cuticle. Interseminal scales with the same characters were obtained from both specimens (Pl. 12, fig. 51). The interseminal scales, 1·5 to 2 mm. in diameter, are, in general, conical with rounded apex or more or less polygonal in outline. The cells are thick-walled and arranged concentrically they measure 40 to 60 μ in length by 20 to 40 μ in width. The superficial cell wall is convex or forms a papilla, some cells constitute the base of isolated hairs (Pl. 12, fig. 51; Text-fig. 57). The stomata (Pl. 12, fig. 52; Text-fig. 58) are syndetocheilic and are also arranged concentrically, the guard cells are sunken and the lateral wall heavily cutinized. The outline of the stomatal aperture is distinct. The stomata measure 50 to 60 μ in length and there are about 30 to 50 per sq. mm.

Discussion. It was thought at first that this specimen belonged to *W. bulbiformis*, the umbonate apex of the cone being merely a variation of that species. However, study of the cuticle from the shields showed that they were different. The number of stomata (30 to 50 per sq. mm.) was far greater than that observed in *W. bulbiformis* (2 to 6 per shield) and although the stomata are similar they are larger and are orientated with their longitudinal axes tangential to the contour. In addition the cutinization of the guard cells is heavier, as are the sides of the aperture, delineating the outline of the stomata more clearly. The cell walls in *W. umbonata* are thicker and more irregular, and the hairs and papillae more abundant than in *W. bulbiformis*.

The presence of the central umbo is a feature in common with *Williamsonia pyramidalis* Nathorst (1911 : 24, pl. 5, figs. 9, 10) from the Jurassic of Cloughton Wyke, Yorkshire with which it might be compared if only it were more complete.

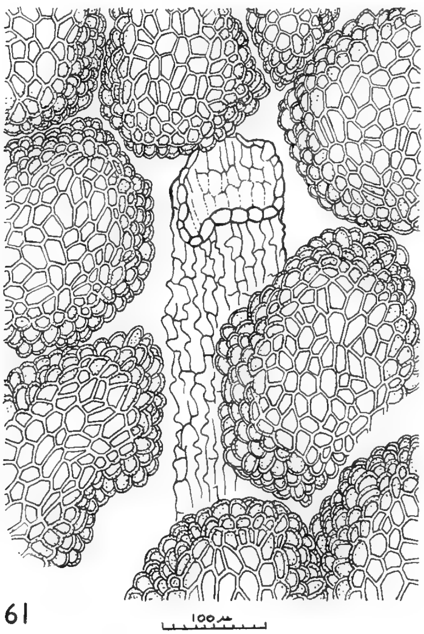
Nathorst considers that the umbo may be the base of attachment of the microsporophylls, which in his material appear to be outlined immediately above the female ' flower '. Without evidence of connexion, however, it is not possible to say whether it is a hermaphroditic ' flower ' or whether the position of the microsporophylls is a result of chance association.

Williamsonia sp.

(Pl. 13, figs. 53–56 ; Text-figs. 59–61)

The single specimen (BAPB 7982) of this undetermined species of *Williamsonia* consists of an external mould of a female cone (gynaecium) of a ' flower ' on the surface of which an almost complete cuticle was preserved.

Viewed from the upper side it is elliptical in shape with a central depression from which emerges a horizontally extended umbo (Text-fig. 59). The greatest diameter



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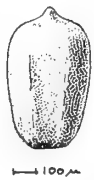

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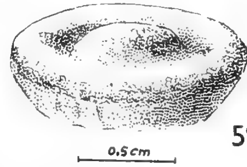

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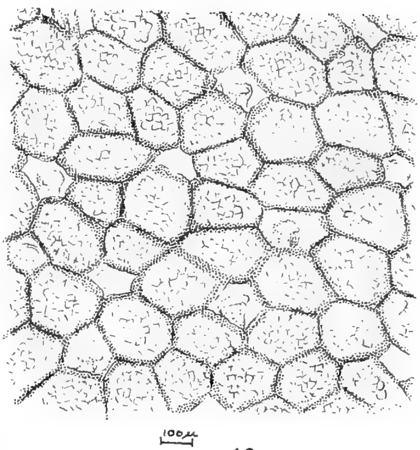

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FIGS. 59–61. *Williamsonia* sp. Fig. 59. Reconstruction of specimen BAPB 7982. Fig. 60. General aspect of cuticle, showing arrangement of interseminal scales and micropyles. BAPB 7982. Fig. 61. Micropylar tube with papillose surface, surrounded by interseminal scales. BAPB 7982.

FIG. 62. Immature seed of *Williamsonia*. BAPB 7938

of the cone is 11 mm. and the smallest 7 mm. at the margins, it is 3·5 mm. high. There are no remains of bracts.

Impressed on the surface of the specimen are the polygonal outlines of the interseminal scales (Pl. 13, fig. 54), generally with 5–6 sides, and from 200–280 μ in maximum diameter. Five or six interseminal scales surround the micropyle. Towards the margins the interseminal scales enlarge and lengthen tangentially until they reach 5 or 6 times the size of the central scales.

Cuticle. The cuticle of the interseminal scales and of the micropyles has been perfectly preserved and remain united. The cell walls of the interseminal scales (Pl. 13, figs. 55, 56 ; Text-fig. 61) are straight, thick, bulging, from 15 to 38 μ in length and 10 to 20 μ in breadth. Stomata were not observed. The micropylar tube is a little more than 100 μ wide and shows rectangular papillose cells that are lengthened longitudinally.

Discussion. This specimen may be a young individual of one of the *Williamsonia* species already described, but the well formed structure of the interseminal scales and micropyle would indicate that it belongs to a small well developed ' flower ' and for this reason and in the absence of diagnostic characters it seems preferable to leave it unnamed.

Immature seeds of ***Williamsonia***

(Pl. 13, fig. 57 ; Text-fig. 62)

On specimen BAPB no. 7938, associated with fragments of large interseminal scales, megasporophylls and parts of the axis of a ' flower ' or fruit of *Williamsonia*, there is a series of small hollows many of which contain small carbonaceous bodies with a well-defined prismatic hexagonal or pentagonal shape.

These bodies are probably the remains of immature seeds of *Williamsonia*. The size of the previously recorded seeds of *Williamsonia* is from 4 to 6 mm. in length and 2·5 mm. in breadth (*W. bucklandi* and *W. gigas*) as compared with 0·5 to 0·7 mm. in length and 0·3 to 0·5 mm. in breadth of the specimens from Ticó.

In the specimens of *Williamsonia umbonata* and *W. bulbiformis* there are megasporophylls measuring up to 3 and 3·5 mm. in width respectively, which would indicate the presence of seeds of approximately the same size as those of other species.

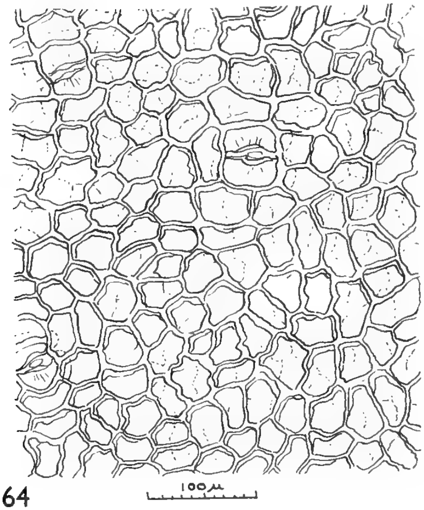
The shape of the seed is prismatic hexagonal or pentagonal, slightly narrowed towards the base with its ends rounded and in some specimens umbonate. Oxidization of the material only yields very small fragments of cuticle, possibly from the integument, without visible anatomical structure.

Genus ***CYCADOLEPIS*** Saporta

Cycadolepis coriacea sp. nov.

(Pl. 14, Pl. 15, figs. 63–65 ; Text-figs. 63–68)

Diagnosis. Bract large, typically oblong or oval-lanceolate, length typically 63 mm. × 30 mm., abaxial side strongly convex, margins incurved and close to one



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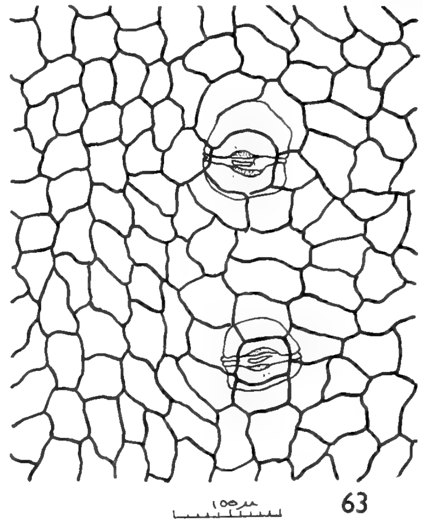

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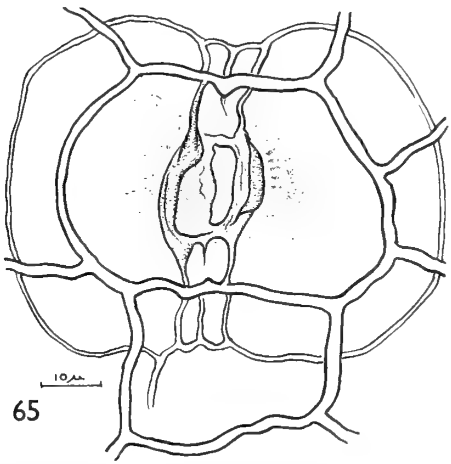

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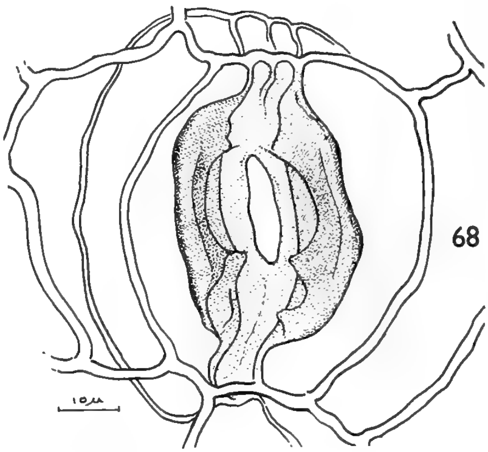

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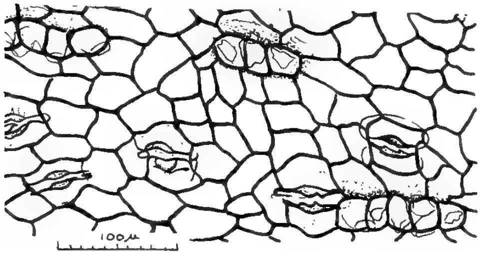

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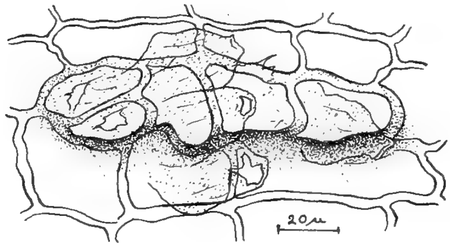

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FIGS. 63–68. *Cycadolepis coriacea* sp. nov. Fig. 63. Adaxial epidermis with transverse stomata. B.M. (N.H.), V.45384. Fig. 64. Abaxial epidermis with thick-walled cells, sunken stomata and traces of hypodermal cells. B.M. (N.H.), V.45384. Fig. 65. Stoma from adaxial epidermis. B.M. (N.H.), V.45384. Fig. 66. Abaxial epidermis showing grouped hairs. BAPB 7924. Fig. 67. Details of grouped hairs. BAPB 7924. Fig. 68. Stoma of marginal region of bract. BAPB 7928.

another in the upper part ; base wide, line of insertion nearly straight. Veins nearly parallel in middle part, forking and anastomosing and curving outwards to the margins.

Abaxial cuticle thick, cells nearly isodiametric but elongated parallel with the veins in middle region and towards the margins, anticlinal walls very broad, nearly straight, surface wall flat.

Stomata scattered, orientated transversely to the veins ; whole apparatus somewhat sunken and poles of guard cells and outer margins of subsidiary cells overlapped by surrounding epidermal cells. Subsidiary cell surface showing transverse striae, no papillae present. Hypoderms present and slightly cutinized, composed of cells of about the same size as the epidermal cells. Trichome bases frequent, consisting of a transverse row of 3–6 cells (presumed to bear a flattened scale but free part not known) ; some one-celled trichome bases also present.

Adaxial cuticle less thick, distribution and character of stomata as on abaxial cuticle but number rather less. Cells elongated along the veins but isodiametric or transversely elongated between them. Cells rather larger than on abaxial side, anticlinal walls much thinner, straight or slightly sinuous. Trichome bases absent.

HOLOTYPE. LIL no. 2593.

OTHER MATERIAL. In addition to the holotype, Brit. Mus. (Nat. Hist.) no. V.45384 ; BAPB nos. 7922, 7924 ; LPPB no. 5886.

DESCRIPTION. Five fairly similar specimens were studied. The holotype is the most complete, but some of the others show the base better ; this may be flat or distinctly incurved. The cuticle varies a good deal in different parts of the scale, thus there are no stomata near the base of the adaxial side and the stomata, orientated transversely to the veins, become parallel towards the margins. The cells are straighter walled in some parts than others.

COMPARISON. See *C. involuta.*

Cycadolepis involuta sp. nov.

(Pl. 16, ? Pl. 15, fig. 66 ; Text-figs. 69–76)

DIAGNOSIS. Bract oblong but appearing more or less oval through incurving of margins ; typically 4·5 cm. × 2·5 cm. Veins longitudinal in middle part but curving out to meet margins at a right angle ; veins forking and anastomosing ; vein concentration near margin about 12 per cm.

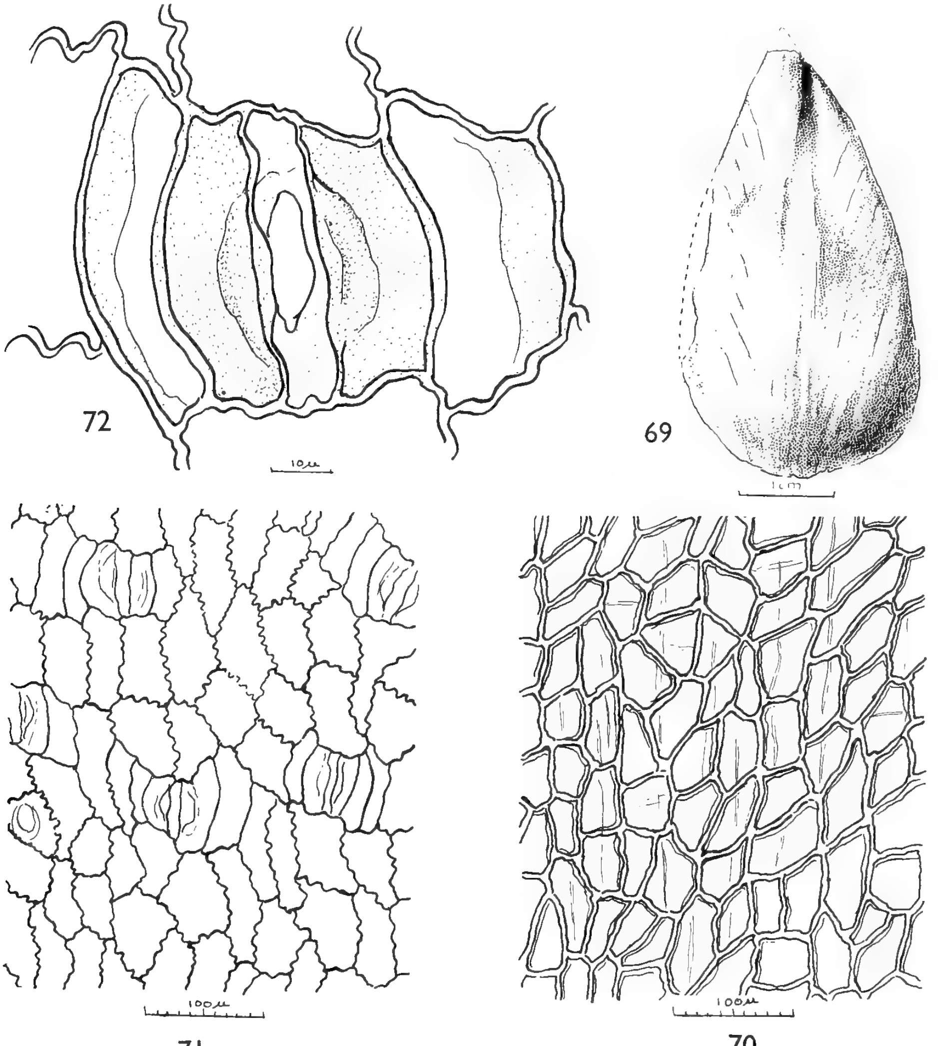
Abaxial cuticle showing polygonal or rectangular cells tending to form longitudinal files. Anticlinal walls distinctly and rather finely sinuous, cell surface often showing a small, hollow papilla. Unicellular trichome bases frequent in some regions. Stomata frequent, orientation variable or transverse to files of epidermal cells. Subsidiary cells rather small, surface thickened ; encircling cells often present opposite outer walls of subsidiary cells.

Adaxial cuticle thicker than abaxial. Cells tending to be rectangular and to form longitudinal files. Anticlinal walls thick, straight or nearly straight. Cell surface

flat. Stomata scarce but as on abaxial surface. Slightly cutinized, elongated hypodermal cells present.

Holotype. LIL 2594. Text-figs. 69–72.

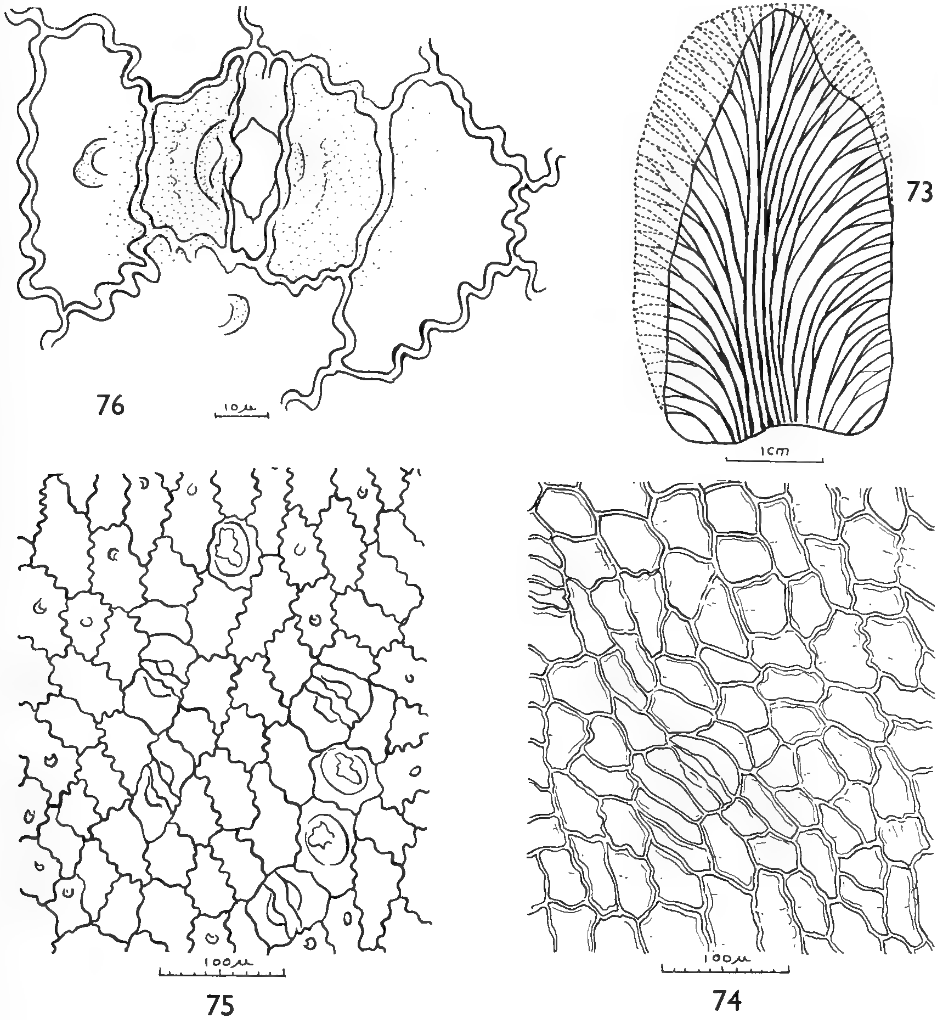
Other material. In addition to the holotype, BAPB no. 7910.



Figs. 69–72. *Cycadolepis involuta* sp. nov. Fig. 69. Specimen with folded apex. Holotype, LIL 2594. Fig. 70. Adaxial epidermis, showing traces of hypodermal cells. LIL 2594. Fig. 71. Abaxial epidermis with stomata. LIL 2594. Fig. 72. Stoma of the same abaxial epidermis.

Description. Two satisfactory specimens are known and both are figured. In addition there is the specimen shown in Pl. 15, fig. 66 which is preserved in a sandy matrix and being without a cuticle is not determined with assurance.

Comparison. *C. involuta* looks like *C. rugosa* (Halle)—see Halle (1911) and Harris



Figs. 73–76. *Cycadolepis involuta* sp. nov. Fig. 73. Reconstruction of specimen BAPB 7910. Fig. 74. Cuticle of the adaxial epidermis with few stomata. BAPB 7910. Fig. 75. Cuticle of the abaxial epidermis showing stomata, small papillae and trichome bases. BAPB 7910. Fig. 76. Stoma of the abaxial epidermis. BAPB 7910.

(1953), but its cuticle is very different. *C. rugosa* does not show sinuous walled cells with papillae. It also resembles *C. coriacea* and *C.* cf. *jenkinsiana* in the present flora in form though the epidermal cells readily distinguish it. It may be permissible to point out a certain resemblance between this scale and the pinna of a *Dictyozamites* (e.g. *D. crassinervis* or *D. latifolius*) both in the anastomosing veins and in the general character of the abaxial cuticle.

***Cycadolepis* cf. *jenkinsiana* (Tate) Seward**

(Pl. 17; Text-figs. 77–81)

In present material bract very large, shape ovate-spatulate, apex rounded, lower part tapering. Length up to at least 14·5 cm., maximum width about 6 cm. Veins longitudinal in middle region but arching out to lateral margins which they meet at about 45°, forking and anastomosing. especially towards the margins Concentration of veins about 8 per cm. below, increasing to about 14 per cm. above. Longitudinal striae present between veins.

Cuticle of abaxial surface not known. Adaxial cuticle thin; cells irregularly arranged, or in files parallel with the veins; surface often showing a small median papilla; anticlinal walls thin, sinuous. Stomata frequent variably orientated or transverse to the cell files, subsidiary cells fairly large, anticlinal walls smooth or slightly sinuous, surface flat. Trichome bases numerous consisting of a row or double row of rounded cells; scattered unicellular trichome bases also occurring.

Specimen B.M.(N.H.) no. V.45387 showing the bases of two bracts gave good preparations of the adaxial cuticle only, the others gave less good preparations or none. The specimen in Pl. 17, fig. 72 is a bract folded down its middle. The anastomosing veins are clearly seen and also some of the striae. There are in addition a few other specimens preserved in sandstone which show the size and shape but no fine details.

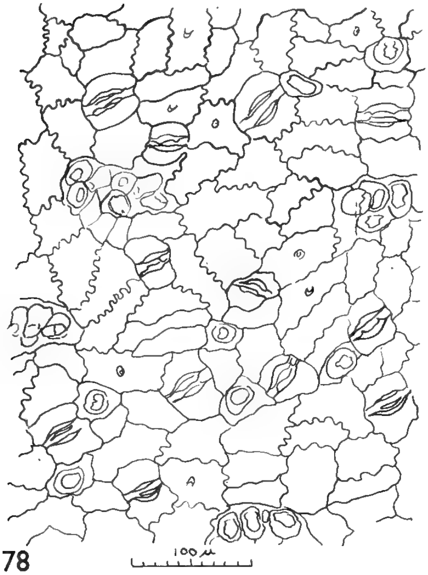
Discussion. The Ticó specimens resemble *C. jenkinsiana* (Tate) from the Wealden of Cape Province (Seward 1903) in form and venation; in particular Seward's pl. 4, fig. 6 is like the specimen shown here in Pl. 17, fig. 72.

Nothing is known about the cuticle of the African specimens so the comparison is incomplete. *C.* cf. *jenkinsiana* is also like large specimens of *C. rugosa* (see Halle 1911, Harris 1953) but in *C. rugosa* the adaxial cuticle has thick straight walls, sunken stomata and no bases of large trichomes.

***Cycadolepis lanceolata* sp. nov.**

(Pl. 18; Text-figs. 82–86)

Diagnosis. Bract lanceolate, somewhat convex, up to 4 cm. × 1·3 cm., bearing marginal hairs up to 9 mm. long in middle part, hairs shorter towards apex and base of bract. Surface faintly marked by about ten longitudinal striations (veins?).



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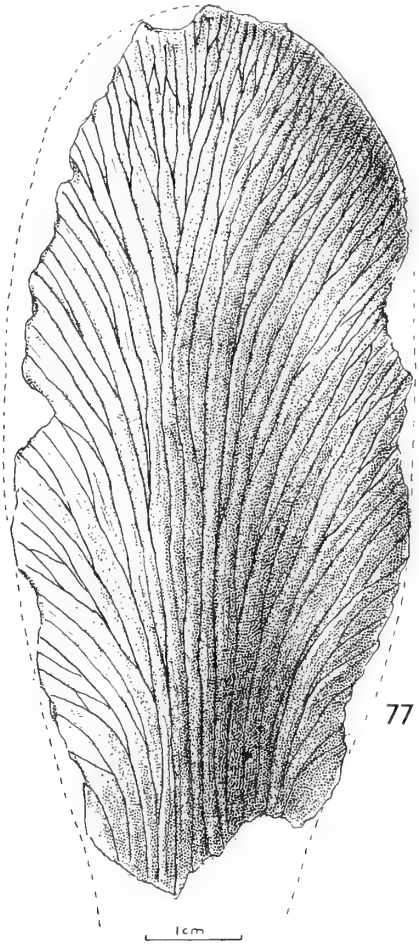

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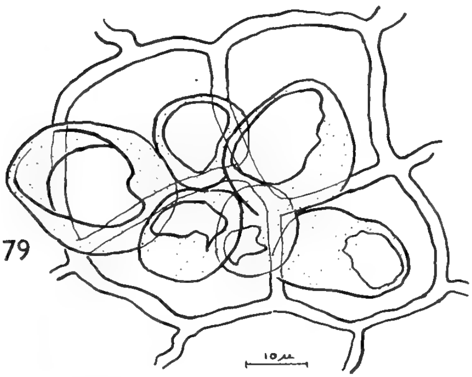

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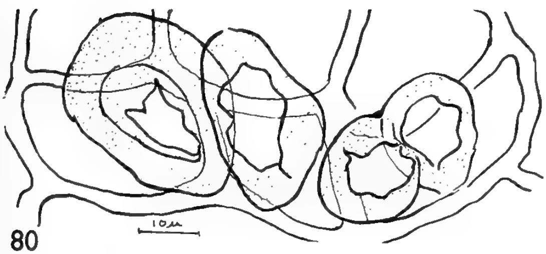

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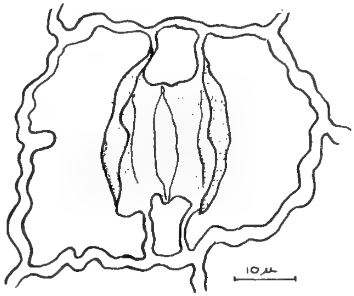

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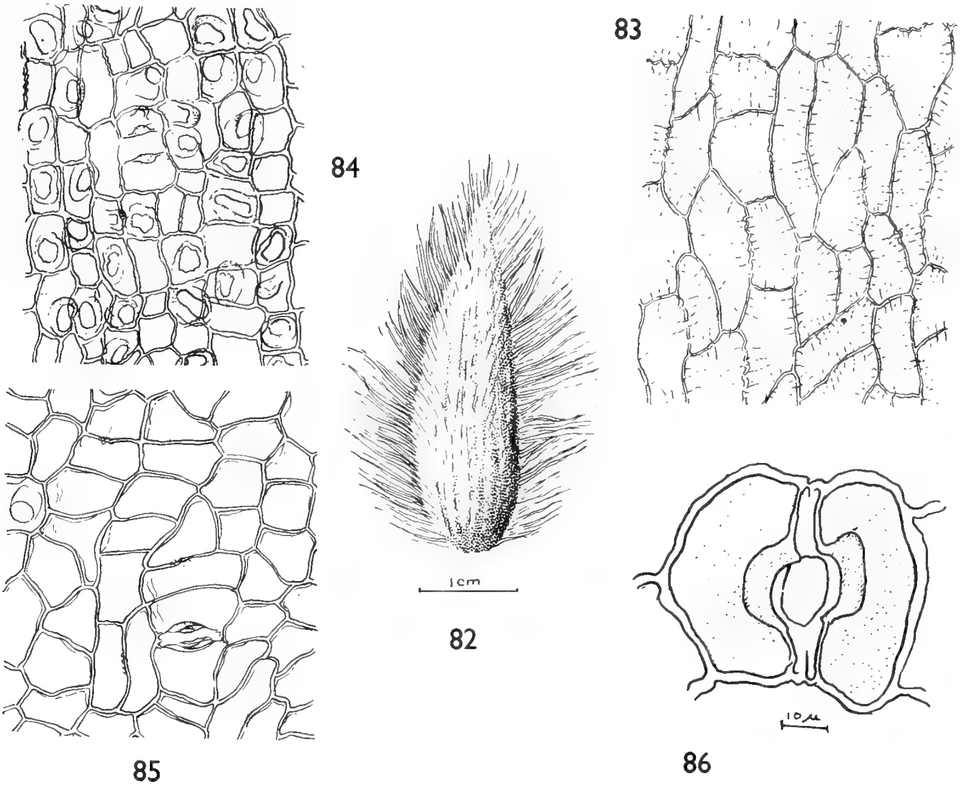
FIGS. 77–81. *Cycadolepis* cf. *jenkinsiana* (Tate) Seward. Fig. 77. Reconstruction of specimen LIL 2592. Fig. 78. Adaxial epidermis showing stomata, small papillae and isolated and grouped hairs. B.M. (N.H.), V.45387. Figs. 79, 80. Details of grouped hairs. B.M. (N.H.), V.45387. Fig. 81. Stoma of the adaxial epidermis. B.M. (N.H.), V.45387.

Abaxial cuticle with numerous stomata. Epidermal cells forming longitudinal files, anticlinal walls straight, fairly thick ; surface wall flat or bearing a large hollow papilla. Trichome bases very numerous and in some parts trichomes arising on every cell ; bases unicellular, rounded. Stomata scattered but transverse to the cell files, subsidiary cells fairly large sometimes bearing a papilla.

Adaxial cuticle similar but cells larger and sometimes showing faint ridges passing from anticlinal walls on to cell surface. Stomata infrequent, trichome bases rare, only exceptionally present.

HOLOTYPE. BAPB no. 7906.



FIGS. 82–86. *Cycadolepis lanceolata* sp. nov. Fig. 82. General aspect of bract with marginal ramentum. BAPB 7906. Fig. 83. Adaxial epidermis with finely sinuate walls and with transverse wrinkles. BAPB 7906. Fig. 84. Abaxial epidermis with numerous hairs, some papillae and stomata. BAPB 7906. Fig. 85. Adaxial epidermis with straight-walled cells, few stomata and hairs. BAPB 7906. Fig. 86. Stoma from abaxial epidermis. BAPB 7906.

Other material. In addition to the holotype, Brit. Mus. (Nat. Hist.) nos. V.45373, V.45386 ; LPPB no. 5884.

Description. The two best specimens are the holotype and the one shown in Pl. 18, fig. 75. Two others are in a sandy rock and have no cuticles preserved.

Comparison. A good many hairy kinds of *Cycadolepis* are known. The following are particularly similar.

C. eriphous Harris (1953) from the Middle Jurassic of Yorkshire is larger and has no stomata on the abaxial cuticle.

C. mexicana Wieland (1914) from the Liassic of Mexico is larger and with longer hairs.

C. johanssoni Harris from the basal Liassic of Greenland and of Sweden (Johansson 1922) as *C. rugosa* is often longer, the surface is rugose and the stomata are orientated longitudinally.

It is interesting that *Williamsonia virginiensis* Fontaine (1889) from the Lower Cretaceous of Potomac shows rather similar bracts. *C. oblonga* described in this work has fewer hairs and no papillae on the adaxial surface. The adaxial cells are longer and the walls thinner and never at all sinuous.

Cycadolepis oblonga sp. nov.

(Pl. 19 ; Text-figs. 87–91)

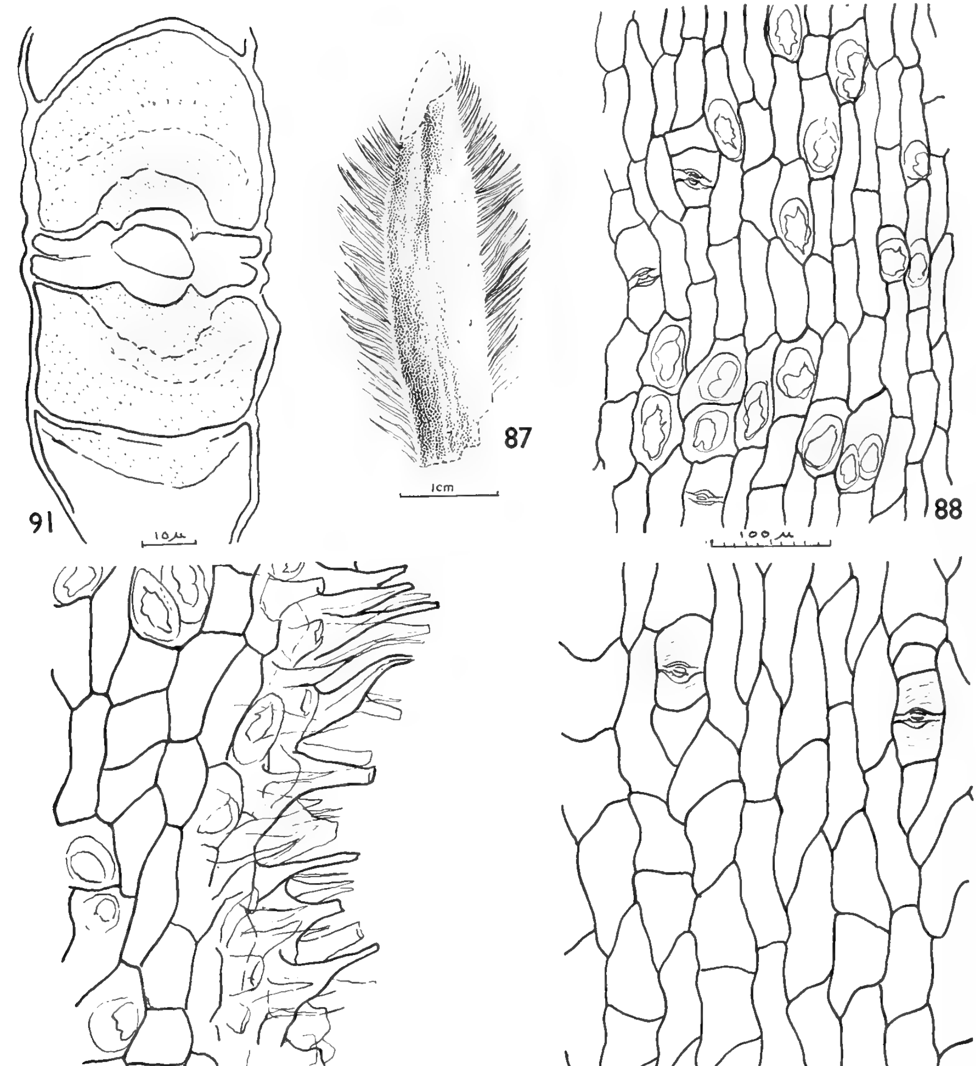
Diagnosis. Bract oblong lanceolate, typically about 4 cm. long × 0·8 cm. wide, width uniform in the lower two-thirds but tapering to the apex. Surface only slightly convex, marked with faint longitudinal grooves. Margins hairy, marginal hairs about 7 mm. long in the middle region but becoming shorter both towards the apex and base of the bract.

Abaxial cuticle showing somewhat elongated cells in longitudinal files, anticlinal walls straight or curved, not sinuous, surface flat. Many cells bearing unicellular trichome bases, and occasional groups of about five side by side, representing broad trichomes or a row of unicellular ones. Stomata frequent, transverse to cell files ; subsidiary cells fairly large, not papillate. Occasionally with lateral encircling cells. Adaxial cuticle showing considerably larger cells of same general shape ; stomata rare ; trichomes absent.

Holotype. BAPB no. 7907. The only specimen.

Description. *C. oblonga* is represented by the holotype alone, a well preserved specimen lacking its extremities ; its original length may have been over 4 cm. It is very like *C. lanceolata* in form and cuticle but it is considered that the differences given above are sufficient to distinguish it.

Comparison Several species are of similar shape and size. *C. spheniscus* Harris (1953) differs in lacking marginal hairs. *C. johanssoni* Harris (1953) from the Greenland Lower Liassic differs in its rugose surface, shorter cells and longitudinal stomata. *C. hirta* Saporta (1875) from the French Upper Jurassic is of unknown structure ; it may be relatively longer.



Figs. 87–91. *Cycadolepis oblonga* sp. nov. Fig. 87. General aspect of bract with marginal ramentum. BAPB 7907. Fig. 88. Abaxial epidermis with trichome bases, cells in longitudinal rows and transverse stomata. BAPB 7907. Fig. 89. Adaxial epidermis with stomata. BAPB 7907. Fig. 90. Details of marginal ramentum. BAPB 7907. Fig. 91. Stoma of adaxial epidermis. BAPB 7907.

III PROBABLE AGE OF THE FLORA

The flora of the Ticó area of Santa Cruz Province, Argentina is rich and well preserved, but many of its genera are new and so are nearly all the species. Three species however have been identified with those of other floras and the generic identification of others throws some light on the age. The three are *Athrotaxis ungeri*, *Ptilophyllum hislopi*, *Cycadolepis jenkinsiana*; the determination of the last two being rather insecure.

Athrotaxis ungeri (Halle) described by Archangelsky (1963) from Ticó has also been recorded from Rio de los Fósiles in the area of Lake San Martin, Santa Cruz Province, which Halle (1913) assigns to the Lower Cretaceous because of its association with strata bearing marine fossils. The species is also represented in the valley of Rio Cardiel overlying beds containing *Crioceras deeckei* from the Barremian (Piatnizky 1938) together with *Nathorstia alata* Halle which also occurs in Rio de los Fósiles. Frenguelli (1949) records *Athrotaxis ungeri* in Canadon Asfalto, Chubut, together with other plants which he assigns to the Bajocian or base of the Lower Calovian and correlates with the Jabalpur Series considered by him to be Dogger, although many authors place this series in the Lower Cretaceous or Upper Jurassic.

Ptilophyllum hislopi is a determination without the advantage of knowledge of the cuticle. In India it occurs in the Rajmahal flora the age of which is not precisely known but it must be between Lower and Upper Jurassic. It also occurs in the (roughly) Middle Jurassic of Graham Land and the Middle Jurassic of Neuquen in Argentina and is recorded from the Lower Cretaceous of India.

C. cf. *jenkinsiana*, is identified (though again without the evidence from the cuticle) with the original specimens from the Wealden of S. Africa.

Of genera which give some rough indications of age we have:

Brachyphyllum with four species. Conifers with this sort of foliage are doubtless of more than one family, but even so it is true that the number of species increases from the Rhaetic onwards and is at a maximum around the Upper Jurassic and Lower Cretaceous.

Dictyozamites according to Jacob (1951) is characteristic of the Middle Jurassic, but it must be remembered that some of the floras in which it occurs are imperfectly dated. It certainly has several species in the Upper Jurassic of Japan, but the only Cretaceous record known to the writer is a doubtful one from S. Africa.

Otozamites which is rare in the Rhaetic increases through the Lower Jurassic to a maximum in the Middle Jurassic. It is still very common in the Upper Jurassic but less so in the Lower Cretaceous.

Zamites is scarcely known with any security before the Middle Jurassic. It extends into the Lower Cretaceous.

Pterophyllum is at a maximum in the Upper Triassic, but it occurs in diminishing numbers up to the Lower Cretaceous. In the Ticó flora it is represented by a single imperfectly known species.

The general inference on the present rather few and sometimes insecure determinations of species and the reliable determinations of genera—which however, have

longer ranges—is that the Ticó flora is younger than Middle Jurassic, but where it lies in the range of Upper Jurassic and Lower Cretaceous is best left until we have more and clearer evidence.

IV ACKNOWLEDGMENTS

I should like to record my sincere thanks to Professor T. M. Harris for much help in the preparation of this work and I am greatly indebted to Mr. F. M. Wonnacott for critically revising the manuscript.

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PLATE 1

Otozamites parviauriculata sp. nov.

FIG. 1. Fragment of frond. Holotype, LIL 2600. ×1.
FIG. 2. Fragment of frond with more elongated pinnae. BAPB 7961. ×1.
FIG. 3. Specimen BAPB 7963. ×1.

Otozamites grandis sp. nov.

FIG. 4. Fragment of frond with imbricate pinnae. Holotype, LIL 2590. ×1.
FIG. 5. Specimen showing details of insertion of pinnae. BAPB 7968. ×2.
FIG. 6. Specimen with large pinnae. BAPB 7964. × 1.

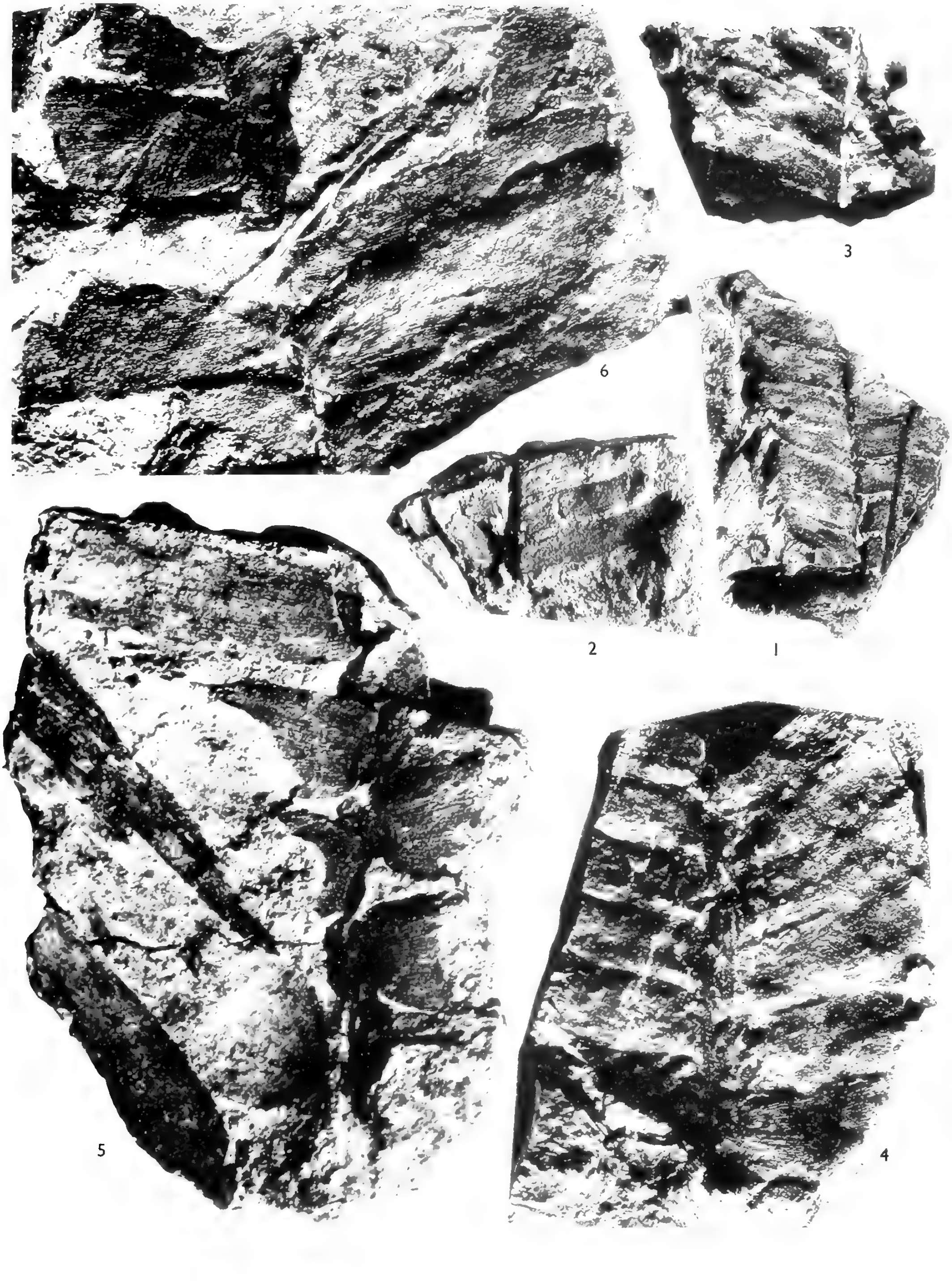
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PLATE 2

Otozamites parviauriculata sp. nov.

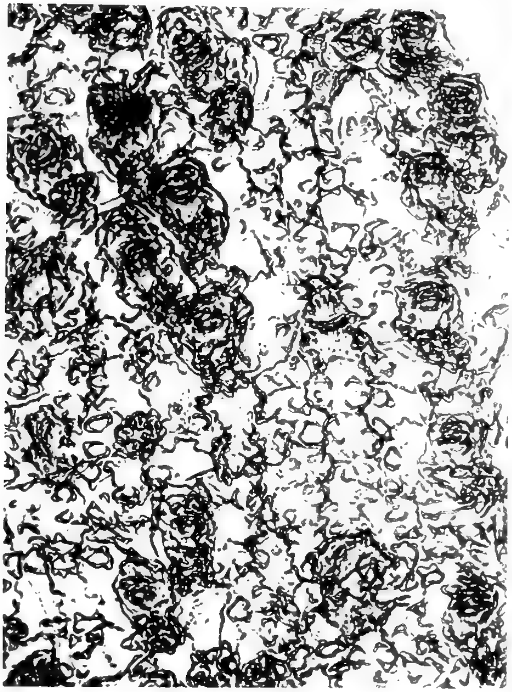
FIG. 7. Cuticle of lower epidermis with stomata aligned in spaces between nerves; hairs and abundant papillae. Holotype, LIL 2600. ×200.

FIG. 8. Stomata sunken in bottom of outer stomatal chamber with its aperture encircled by a crown of papillose cells. Holotype, LIL 2600. ×1000.

Otozamites grandis sp. nov.

FIG. 9. Cuticle of upper (left) and lower epidermis. B.M. (N.H.), no. V.45370, ×200.

FIG. 10. Stomata and papillae. BAPB 7968. ×1000.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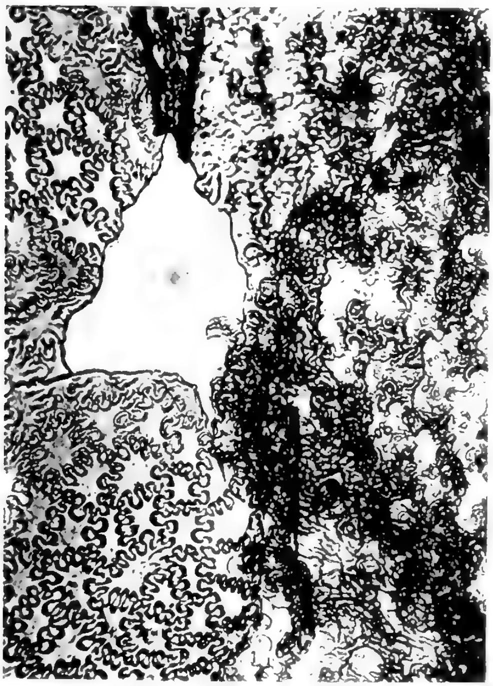
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PLATE 3

Dictyozamites minusculus sp. nov.

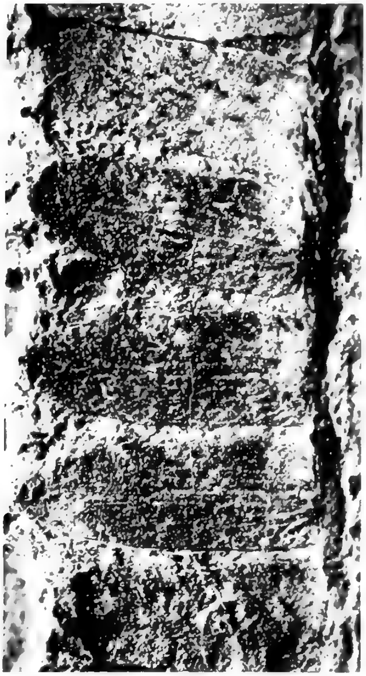
FIG. 11. Enlarged fragment of frond to show details of insertion of pinnae, and nervation. BAPB 7976. ×5.

FIG. 12. Fragment of frond with pinnae preserved on one side. Holotype, LIL 2591. ×2.

FIG. 13. Fragment of frond with alternate pinnae. B.M. (N.H.), no. V.45374. ×2.

FIG. 14. Cuticle of lower epidermis with numerous trichome bases and papillae. BAPB 7971. ×200.

FIG. 15. Stoma with papillae projected over the aperture, trichome bases and papillae. BAPB 7971. ×1000.



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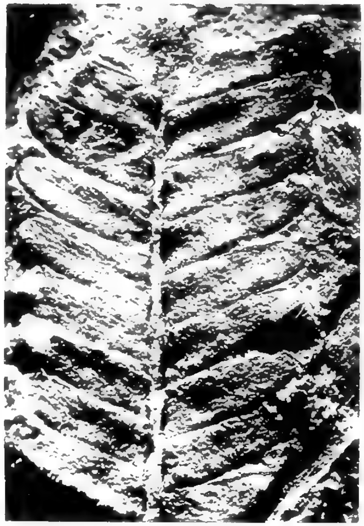

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PLATE 4

Dictyozamites crassinervis sp. nov.

FIG. 16. Part of frond with three fragments of pinnae. Holotype, BAPB 7979. ×1.

Dictyozamites latifolius sp. nov.

FIG. 17. Fragment of frond preserved in a coarse sandstone, with alternate and imbricate pinnae. B.M. (N.H.), no. V.45376. ×1.

FIG. 18. Rubber mould of a pinna showing details of the nerves. BAPB 7917. ×1·5.

FIG. 19. Impression of pinnae on sandstone. BAPB 7916. ×1.

FIG. 20. Impression of pinnae in a tufaceous clay, showing the anastomosing nerves. Holotype, BAPB 7995. ×1.

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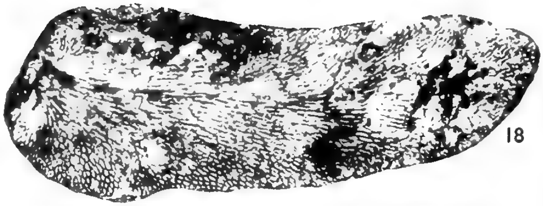

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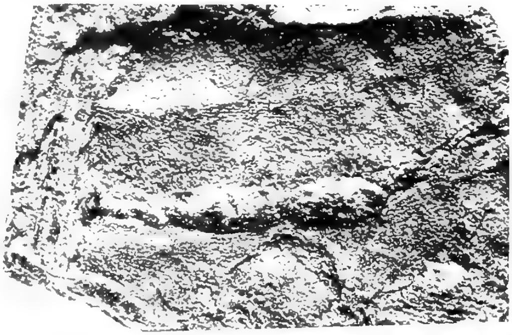

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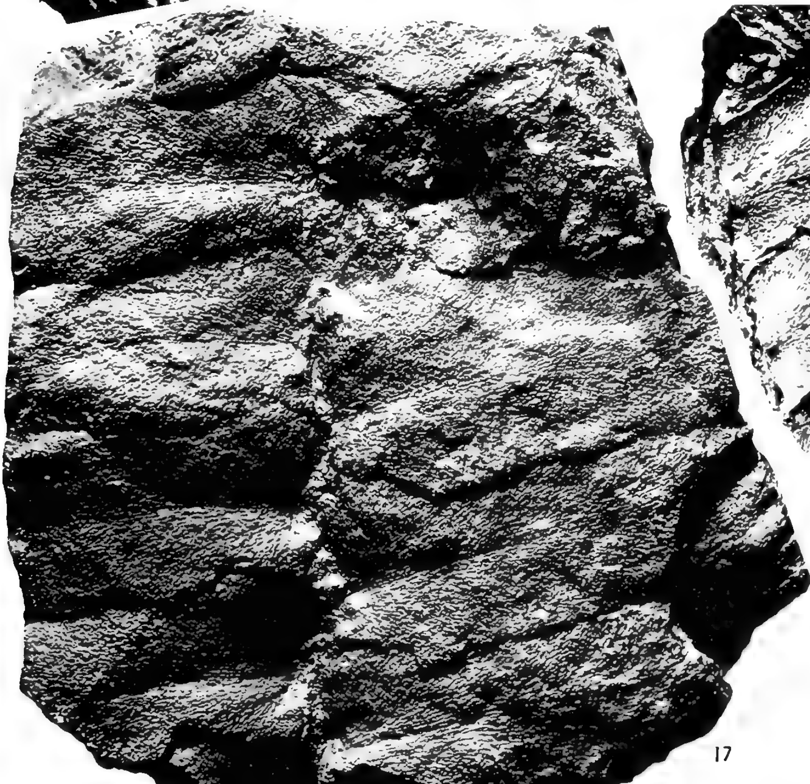

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PLATE 5

Dictyozamites crassinervis sp. nov.

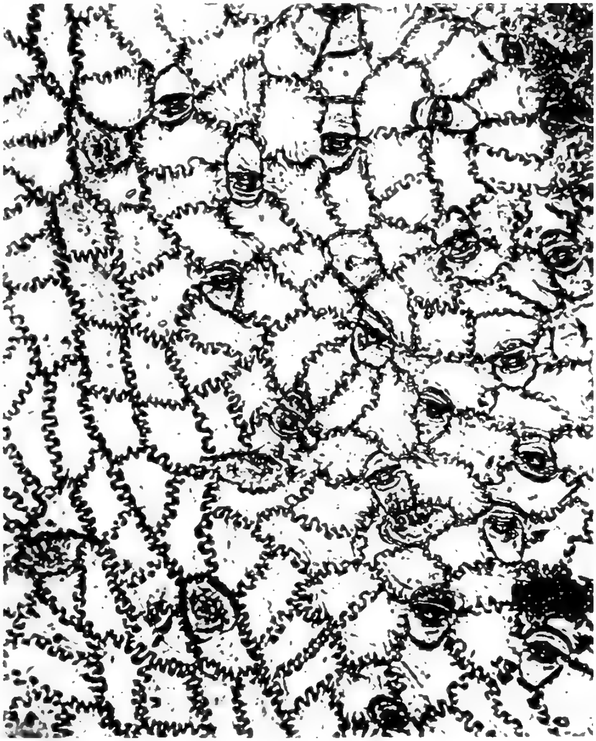
FIG. 21. Cuticle of lower epidermis with longitudinally elongated cells on the nerves (left) and stomata transversely arranged between the nerves. Holotype, BAPB 7979. ×200.

FIG. 22. Stomata from the same specimen, with heavily cutinized subsidiary and guard cells. ×1000.

Dictyozamites latifolius sp. nov.

FIG. 23. Cuticle of lower epidermis with cells elongated longitudinally on the nerves (left). Isodiametric cells and stomata transversely arranged between the nerves. LIL 2597. ×200.

FIG. 24. Stomata encircled by papillae. LIL 2597. ×1000.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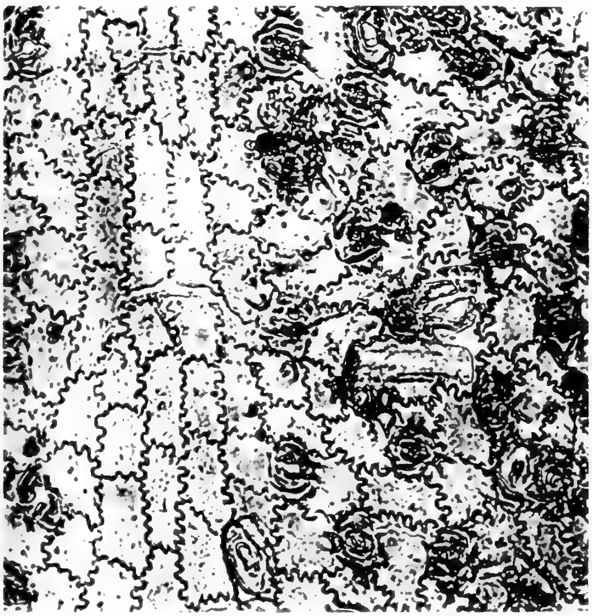
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PLATE 6

Ptilophyllum longipinnatum sp. nov.

FIG. 25. The most complete frond. BAPB 7940. ×1.
FIG. 26. Apical part of a frond. LPPB 5898. ×1.
FIG. 27. Cuticle of lower and upper epidermis. BAPB 7951. ×65.
FIG. 28. Stomata with papillae on the stomatal aperture. BAPB 7956. ×1000.

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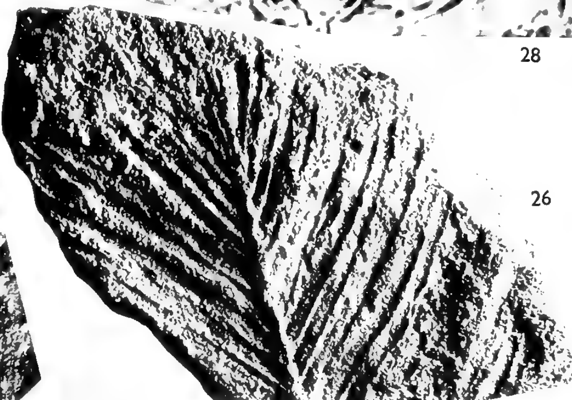

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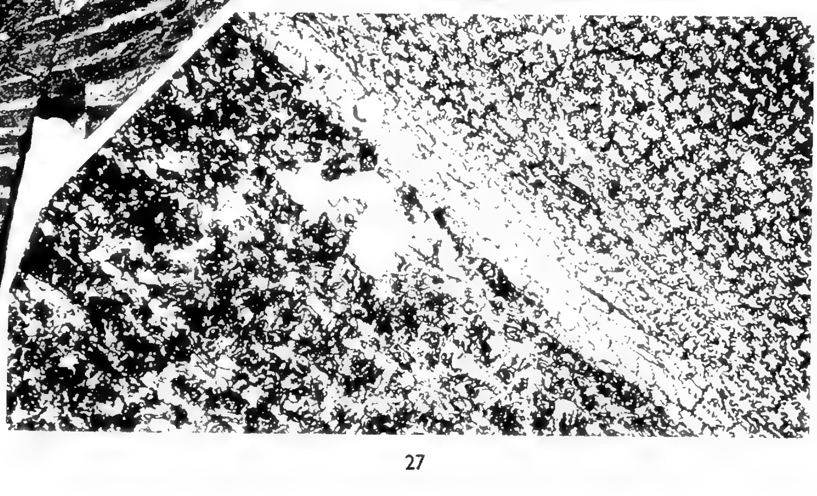

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PLATE 7

Ptilophyllum hislopi (Oldham) Seward

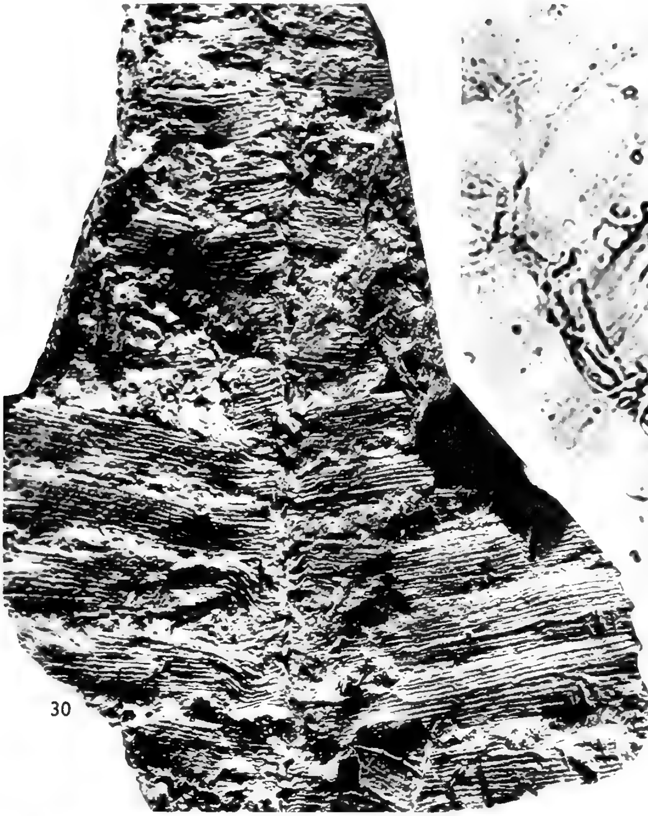
FIG. 29. Impression of a fragment of frond. BAPB 7938. ×1.

Pterophyllum sp.

FIG. 30. Fragment of frond with linear pinnae. BAPB 7959. ×2.

FIG. 31. Cuticle of lower epidermis showing the transversely orientated stomata in the spaces between the nerves, and cells with thickened surface. BAPB 7959. ×200.

FIG. 32. Stoma showing the thickening of the subsidiary cells and small papillae on both sides of the aperture. BAPB 7959. ×1000.



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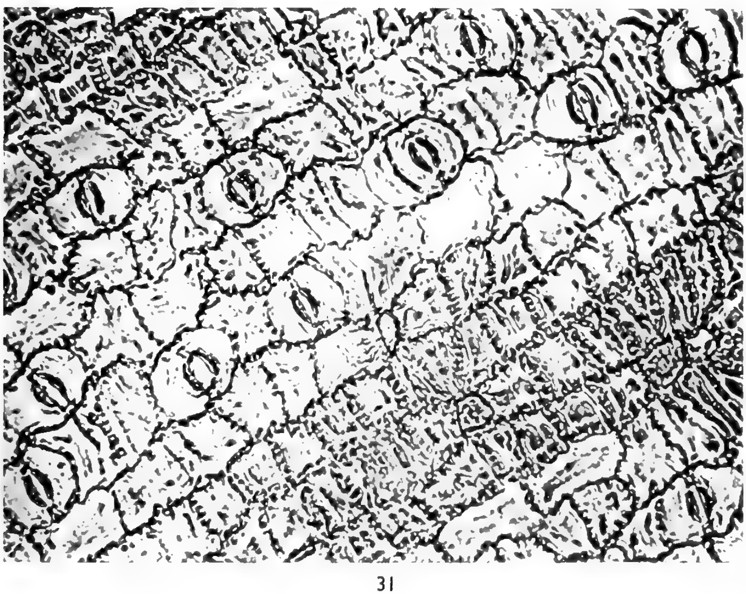

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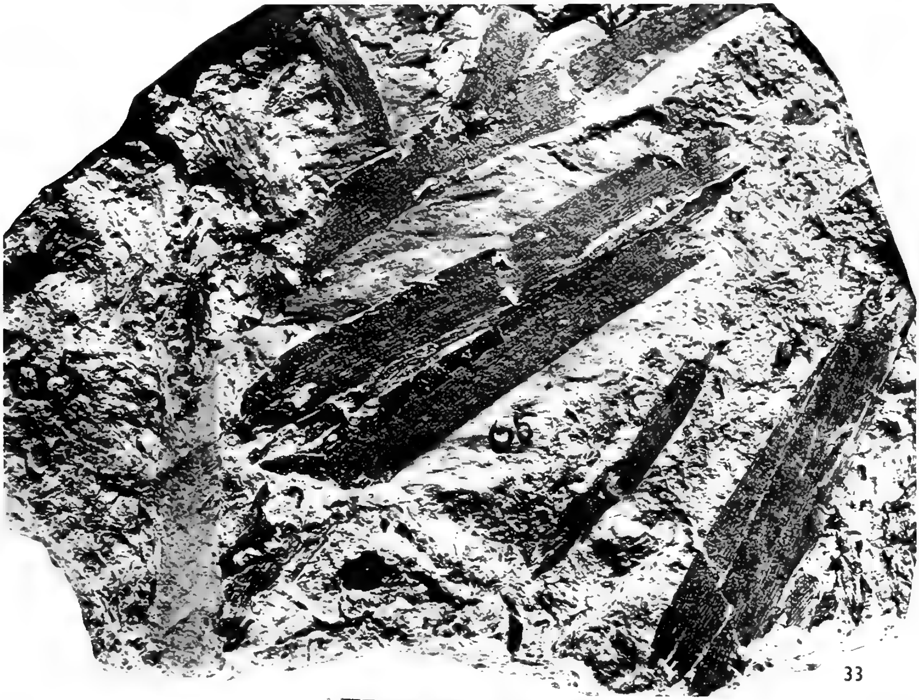
PLATE 8

Zamites decurrens sp. nov.

FIG. 33. The largest specimen. Holotype, LIL 2596. ×1.
FIG. 34. Specimen with proportionally longer pinnae. BAPB 7928. ×1.



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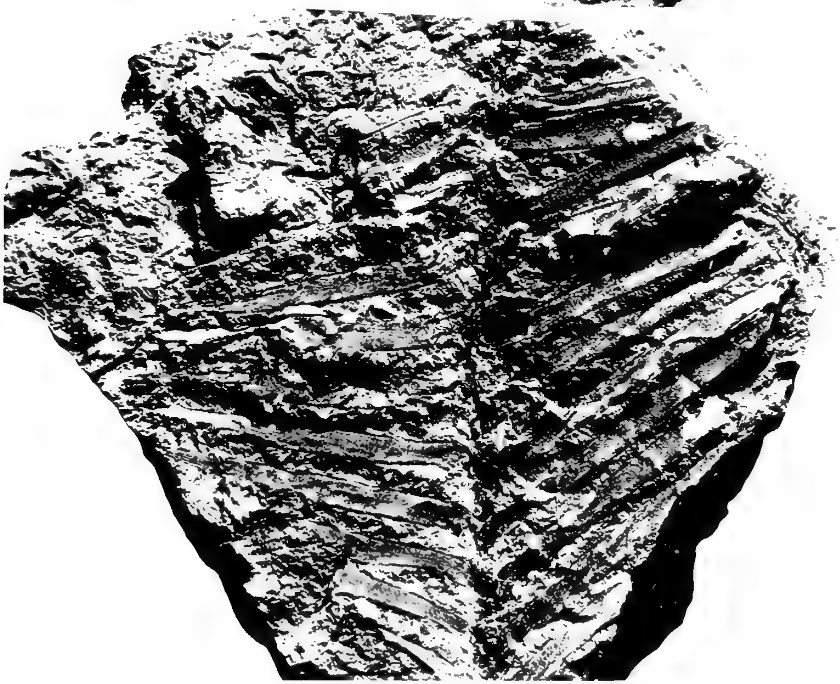

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PLATE 9

Zamites decurrens sp. nov.

FIG. 35. Fragment of a small frond. BAPB 7927. ×2.

FIG. 36. Cuticle of lower epidermis showing globose cells on the nerves; the stomata, hairs and papillae are on the areas between the nerves. A fragment of the upper epidermis can be seen above. BAPB 7927. ×200.

FIG. 37. Fragment of frond showing the pinnae decurrent to the rachis. B.M. (N.H.), no V.45379. ×1.

FIG. 38. Stomata of lower epidermis. BAPB 7927. ×1000.

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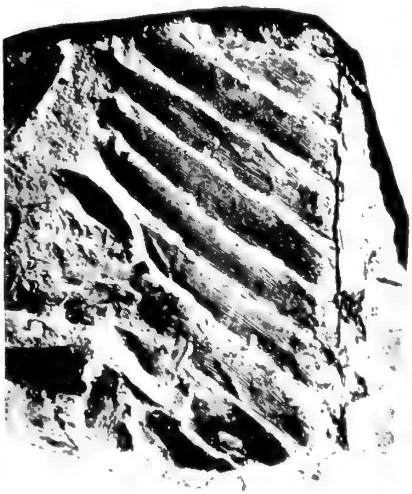

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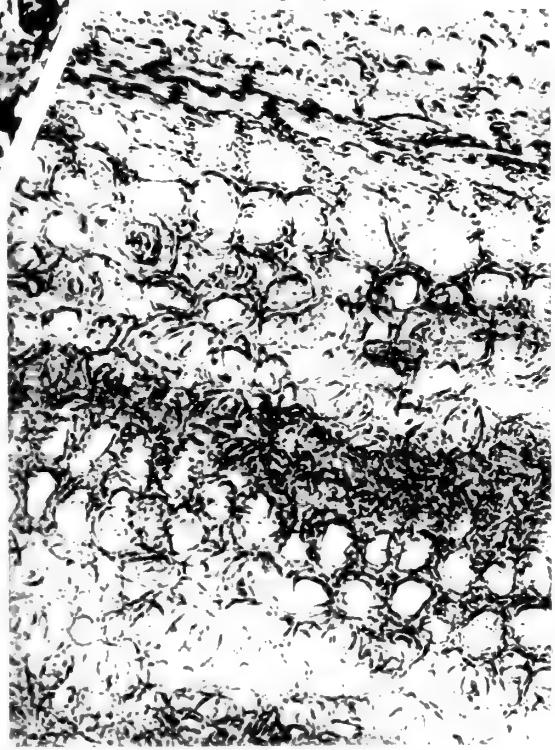

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PLATE 10

Williamsonia bulbiformis sp. nov.

FIG. 39. Basal view of ' flower ' showing in the centre the hollow left by the receptacle surrounded by interseminal scales and bracts. BAPB 7998. ×1.

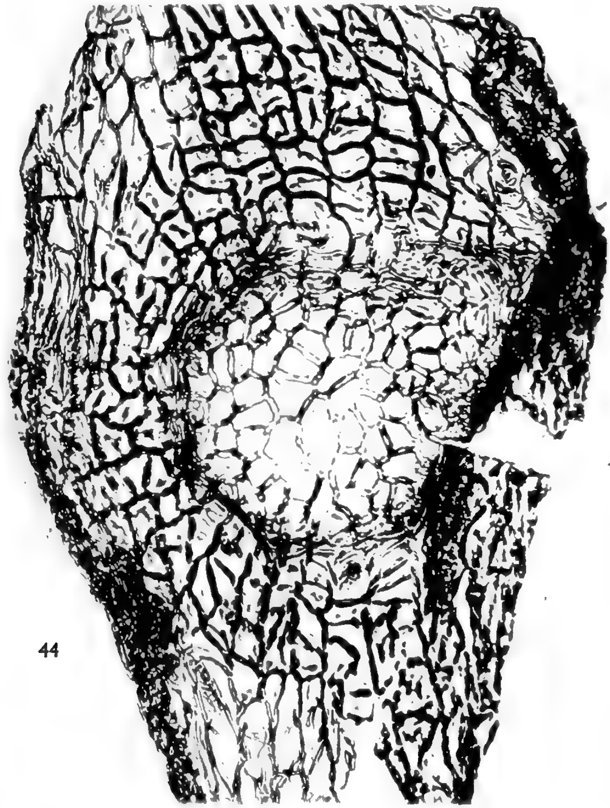
FIG. 40. Same ' flower ' in lateral view. ×1.

FIG. 41. Specimen representing half of a ' flower ' with the hollow of the receptacle, interseminal scales and bracts. B.M. (N.H.), no. V.45381. ×2·5.

FIG. 42. Lateral view of a section of a fertile ' flower ' (fructification). Above, the external mould, below, the casts of fertile megasporophylls and interseminal scales. BAPB 7999. ×2.

FIG. 43. Micropylar tube showing the papillose surface. BAPB 7999. ×200.

FIG. 44. Cuticle of apical portion of interseminal scale (shield) showing central dome and sparse stomata. BAPB 799. ×200.



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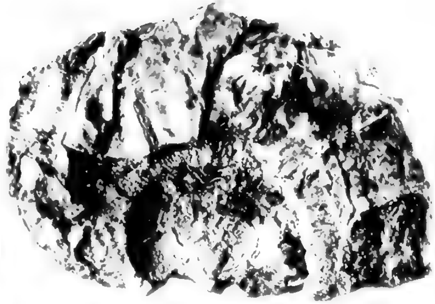

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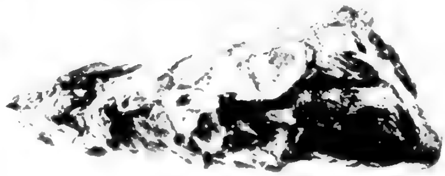

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PLATE 11

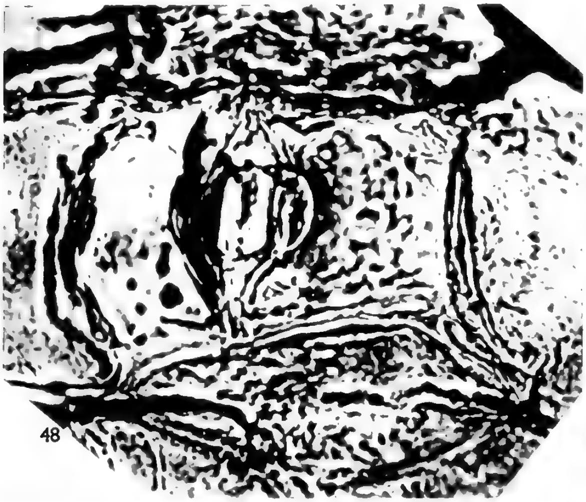
Williamsonia bulbiformis sp. nov.

FIG. 45. Basal part of ' flower ' showing central concave impression of receptacle, surrounded by ring of fertile and sterile megasporophylls and bracts that enclosed the ' flower '. Holotype, LIL 2599. ×2.

FIG. 46. Cuticle of adaxial epidermis of bract. LIL 2599. ×200.

FIG. 47. Cuticle of abaxial epidermis of the same bract showing stomata, some hairs and remains of hypodermal cells. ×200.

FIG. 48. Stoma of abaxial epidermis of bract. LIL 2599. ×1000.



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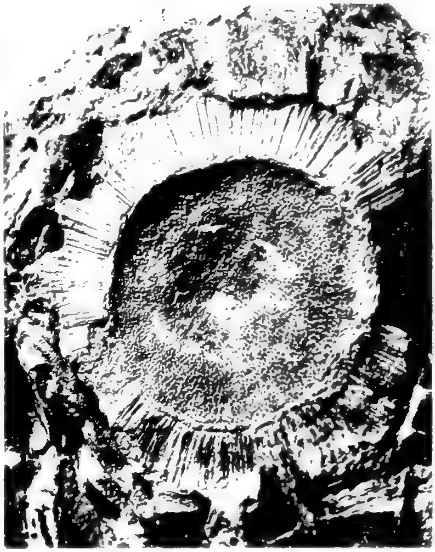

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PLATE 12

Williamsonia umbonata sp. nov.

Fig. 49. Impression of upper part of female cone with apical part of megasporophylls shown in inverse relief, and a central funnel-shaped hollow corresponding to an umbonate apex. Holotype, LIL 2598. ×2.

Fig. 50. Lateral view of specimen BAPB 7997, showing, above, the impression of the upper surface with a funnel-shaped hollow and remains of cuticle, and, in the middle, the impression and casts of megasporophylls. ×2.

Fig. 51. Cuticle of marginal part of shield of an interseminal scale showing hairs and papillose cells. BAPB 7997. ×200.

Fig. 52. Stoma of an interseminal scale. BAPB 7997. ×1000.

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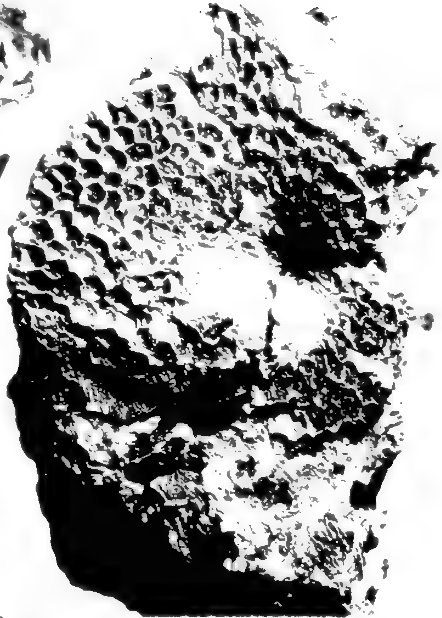

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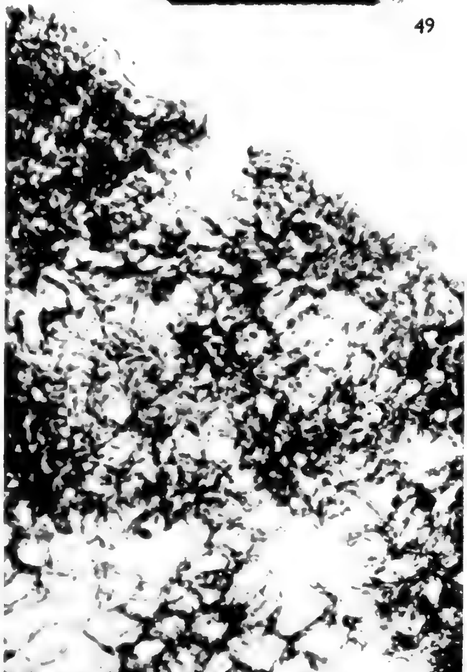

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PLATE 13

Williamsonia sp.

Fig. 53. External mould of female cone (gynaecium) of a 'flower'. BAPB 7982. ×4.

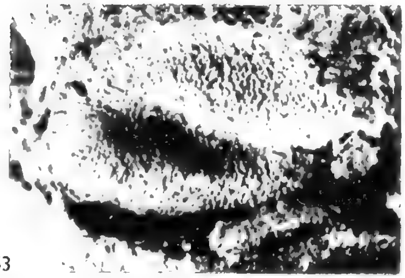
Fig. 54. Same specimen more enlarged showing impressions of interseminal scales. ×7.

Fig. 55. Cuticle of margin of 'flower' with micropyles, surrounded by interseminal scales. The scales of the margin (above) are larger and tangentially elongated. BAPB 7982. ×80.

Fig. 56. Micropylar tube with papillose cells, surrounded by interseminal scales. BAPB 7982. ×200.

Immature seeds of ***Williamsonia***

Fig. 57. Seeds found among fragments of large megasporophylls of *Williamsonia*. BAPB 7938. ×35.



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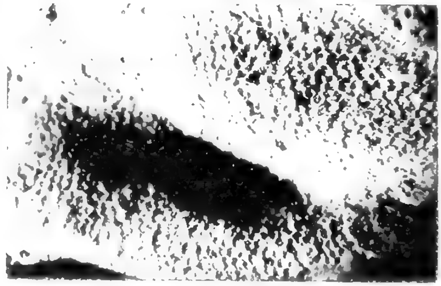

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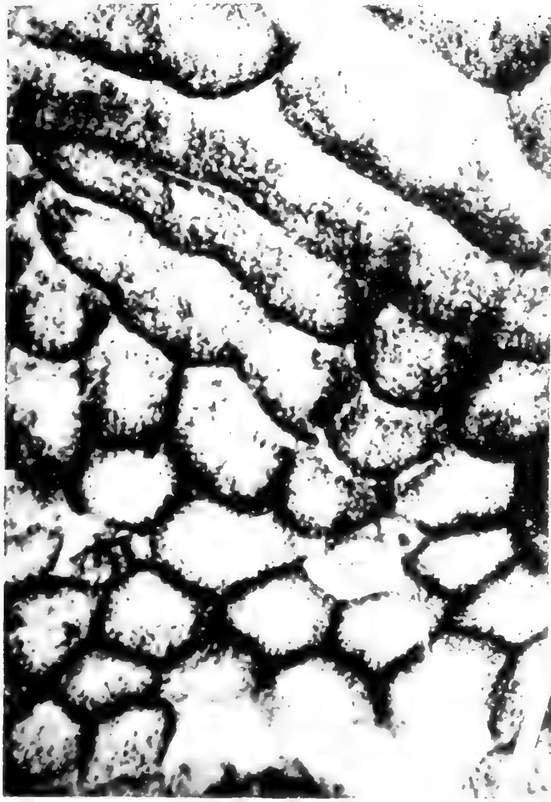

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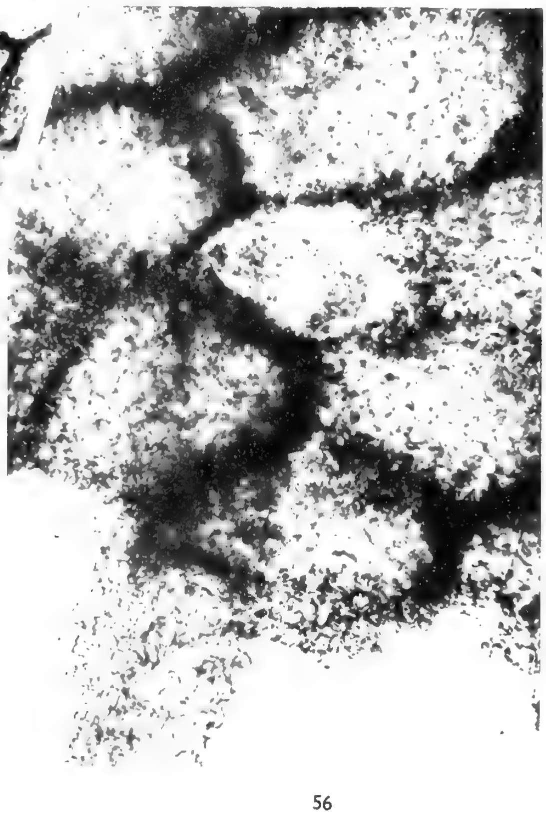

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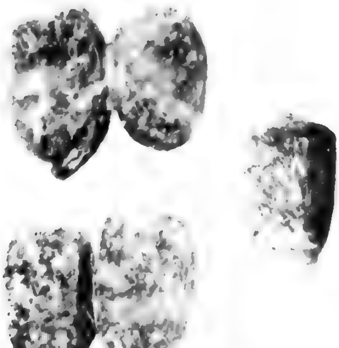

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PLATE 14

Cycadolepis coriacea sp. nov.

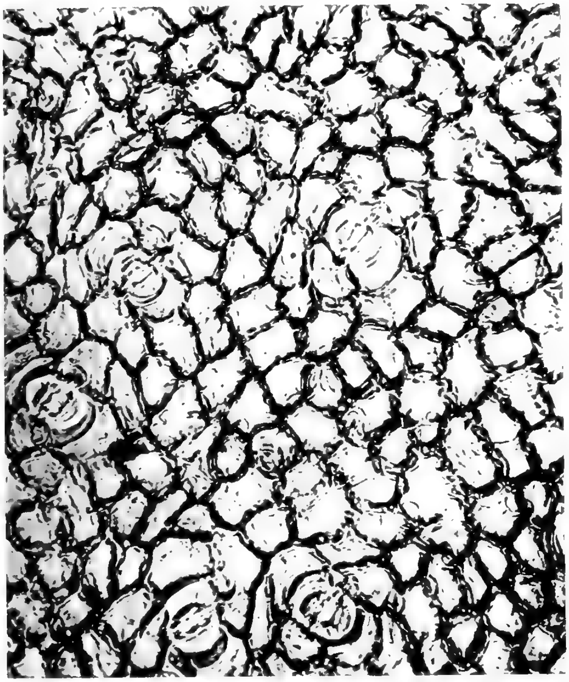
FIG. 58. Basal part of a bract. B.M. (N.H.), no. V.45384. ×2.

FIG. 59. Same specimen. ×1.

FIG. 60. Cuticle of abaxial epidermis with thick-walled cells and sunken stomata. B.M. (N.H.), no. V.45384. ×200.

FIG. 61. Cuticle of adaxial epidermis. B.M. (N.H.), no. V.45384. ×200.

FIG. 62. Stoma of abaxial epidermis. B.M. (N.H.), no. V.45384. ×1000.



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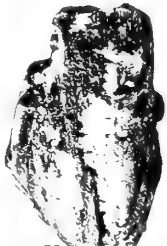

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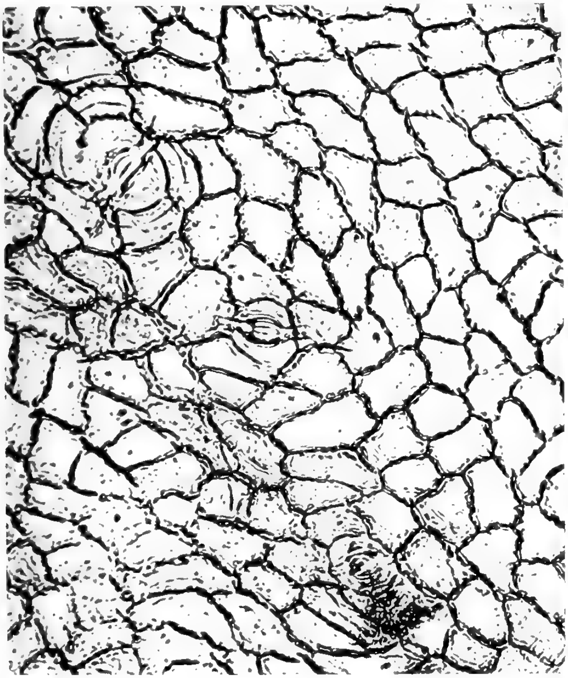

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PLATE 15

Cycadolepis coriacea sp. nov.

FIG. 63. General aspect of bract. LIL 2593. ×2.
FIG. 64. Same specimen. ×1.
FIG. 65. Cuticle of abaxial epidermis showing grouped hairs and stomata. BAPB 7924. ×200.

? *Cycadolepis involuta* sp. nov.

FIG. 66. Specimen from sandy sediment without cuticle. BAPB 7912. ×1.

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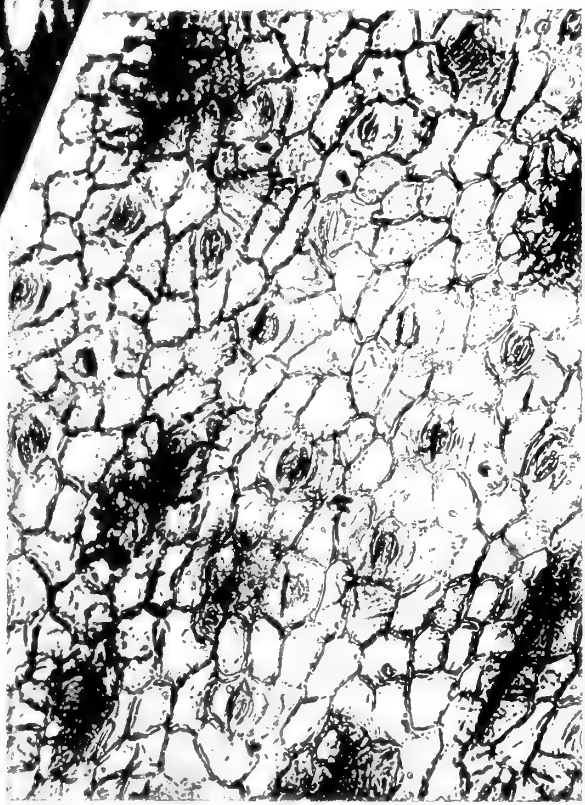

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PLATE 16

Cycadolepis involuta sp. nov.

FIG. 67. General aspect of bract. BAPB 7910. ×2.
FIG. 68. Same specimen. ×1.
FIG. 69. Cuticle of adaxial epidermis. BAPB 7910. ×200.
FIG. 70. Stoma of abaxial epidermis. BAPB 7910. ×1000.
FIG. 71. Cuticle of abaxial epidermis, showing stomata, small papillae and hair bases. BAPB 7910. ×200.

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PLATE 17

***Cycadolepis* cf. *jenkinsiana* (Tate) Seward**

FIG. 72. Half lateral part of a bract folded in the middle. BAPB 7915. $\times 1$.

FIG. 73. Cuticle of adaxial epidermis with stomata, sparse small papillae, isolated hairs and grouped hairs. B.M. (N.H.), no. V.45387. $\times 200$.

FIG. 74. Stoma and grouped hairs. B.M. (N.H.), no. V.45387. $\times 1000$.

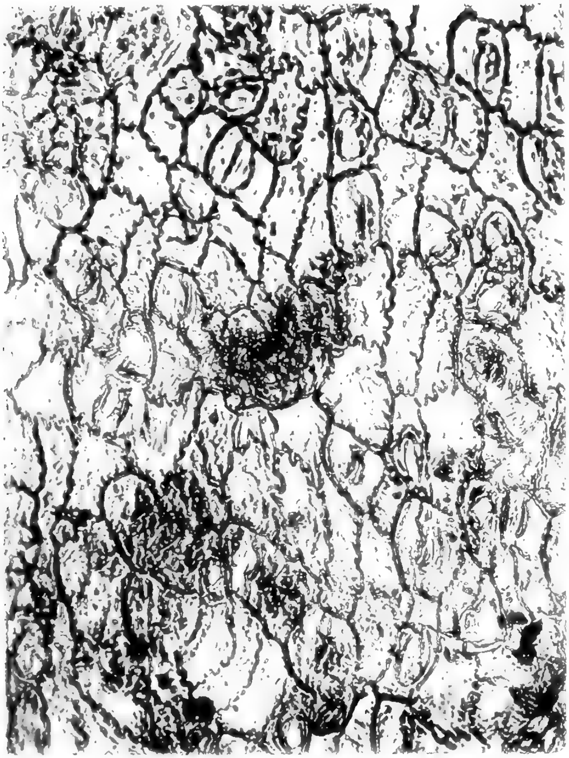

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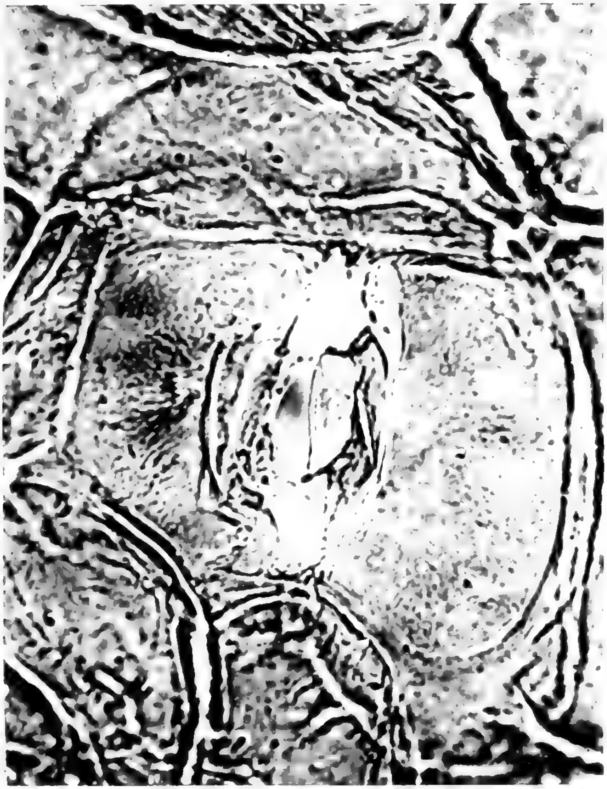
PLATE 18

Cycadolepis lanceolata sp. nov.

FIG. 75. General aspect of bract, with marginal hairs. B.M. (N.H.), no. V.45386. $\times 1$.
FIG. 76. General aspect of holotype. Holotype, BAPB 7906. $\times 1{\cdot}5$.
FIG. 77. Same specimen. $\times 1$.
FIG. 78. Cuticle of adaxial (left) and abaxial (right) epidermis of holotype. $\times 200$.
FIG. 79. Stoma of abaxial epidermis of holotype. $\times 1000$.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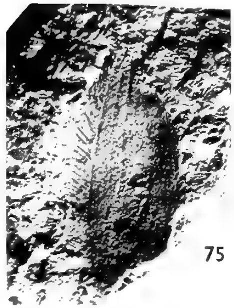
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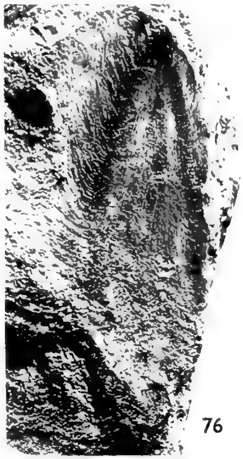
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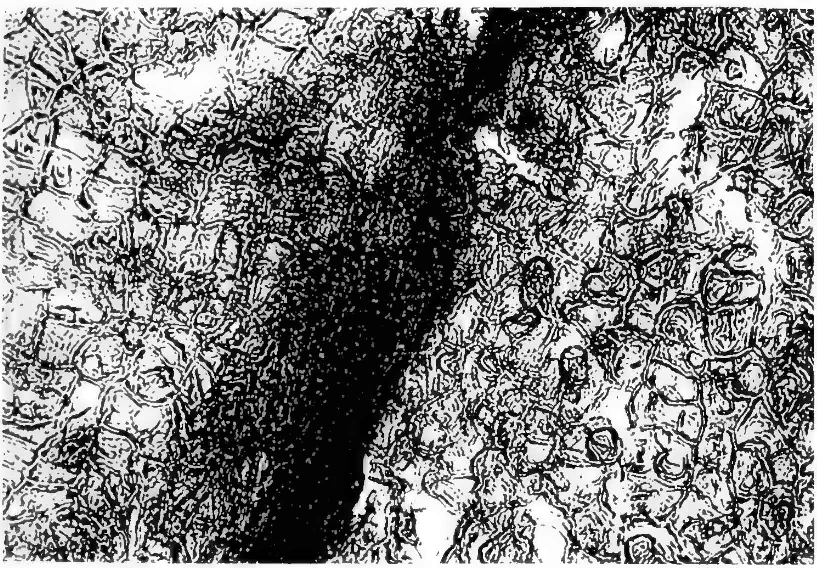
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PLATE 19

Cycadolepis oblonga sp. nov.

FIG. 80. General aspect of bract with marginal ramentum. Holotype, BAPB 7907. ×2.

FIG. 81. Same specimen. ×1.

FIG. 82. Cuticle of adaxial epidermis with cells in longitudinal rows and transverse stomata. BAPB 7907. ×200.

FIG. 83. Cuticle of the abaxial epidermis of same specimen, with trichome bases, stomata and marginal trichomes (above). ×200.

FIG. 84. Stoma and trichome bases (above) of abaxial epidermis. BAPB 7907. ×1000.

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FOSSIL MAMMALS OF AFRICA
No. 20

FOSSIL ANTILOPINI OF EAST AFRICA

A. W. GENTRY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 12 No. 2
LONDON: 1966

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FOSSIL ANTILOPINI OF EAST AFRICA

BY

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(formerly Department of Zoology, Oxford University)

Pp. 43–106 ; 9 *Plates* ; 15 *Text-figures*

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FOSSIL MAMMALS OF AFRICA

No. 20

FOSSIL ANTILOPINI OF EAST AFRICA

By ALAN WILLIAM GENTRY

CONTENTS

SYNOPSIS

Up to five or even more gazelline antelopes are known from Beds I and II at Olduvai Gorge, Tanganyika, but only two of them can be assigned to named species—these are *Phenacotragus recki* (Schwarz) and *Gazella wellsi* Cooke. Both these forms are more closely related to the South African springbok, *Antidorcas marsupialis* (Zimmermann) than to typical gazelles, but less well preserved fossils at Olduvai belong to *Gazella* and are not related to the springbok. It is suggested that *Aepyceros* Sundevall be removed from the Antilopini to the Alcelaphini.

I. INTRODUCTION

Olduvai Gorge is in the Serengeti Plains of North West Tanganyika near latitude 3° S. and longitude 35° E. A revised account of the stratigraphy and palaeontology has been published by Leakey (1965); all that need be said here is that four beds, mostly arising from deposition in a lake or lakes, are present above a basaltic lava flow in the bottom of the gorge. On the basis of faunal correlations and potassium argon dating, Bed I is most likely to be contemporary with the Upper Villafranchian (Lower Pleistocene) of Eurasia. The transition from Bed I to lower II does not involve so great a faunal change as that between the lower and the upper parts of Bed II; above this latter break the Olduvai beds appear to belong to the Middle Pleistocene. The gorge itself was formed fairly recently, and the fossils dealt with here are practically all from living floors of Beds I and II.

The digging sites are referred to by combinations of initials, e.g. SHK, BK, FLK. At any site excavations may have been made at a number of horizontal levels, and

these are indicated by arabic numerals following the roman numeral for the bed. In a sequence of site layers within a single bed, lower numbers are later in time than higher numbers, which is the reverse of the method used in numbering the beds themselves. The layers 1–5 of site FLKN I excavated in 1960 are just below the top of Bed I and some 20 feet higher than site FLK (Leakey 1960). The fauna of FLKN I appears to show a drier climate than at the earlier sites. The age of FLK I is about 1·75 million years, and estimates nearer the top of Bed I were 1·02, 1·13 and 1·38 million years (Leakey, Evernden & Curtis 1961). A reference on a fossil to several layers, e.g. " layers 1–2–3 " indicates that there had been a fall of the layers caused by a storm during excavation, so that the original layer from which the fossil came is unknown. Excavations at the sites SHK and BK in Bed II are in the upper part of that bed, that is after the major faunal change.

The fossils studied are in the National Museum's Centre for Prehistory and Palaeontology in Nairobi and the British Museum (Natural History), London. The latter collection contains fossils excavated until 1935, and the Nairobi collection those excavated thereafter. Specimens in the British Museum (Natural History) are referred to by their registered numbers and bed of origin, and those in Nairobi by their year of excavation and site number.

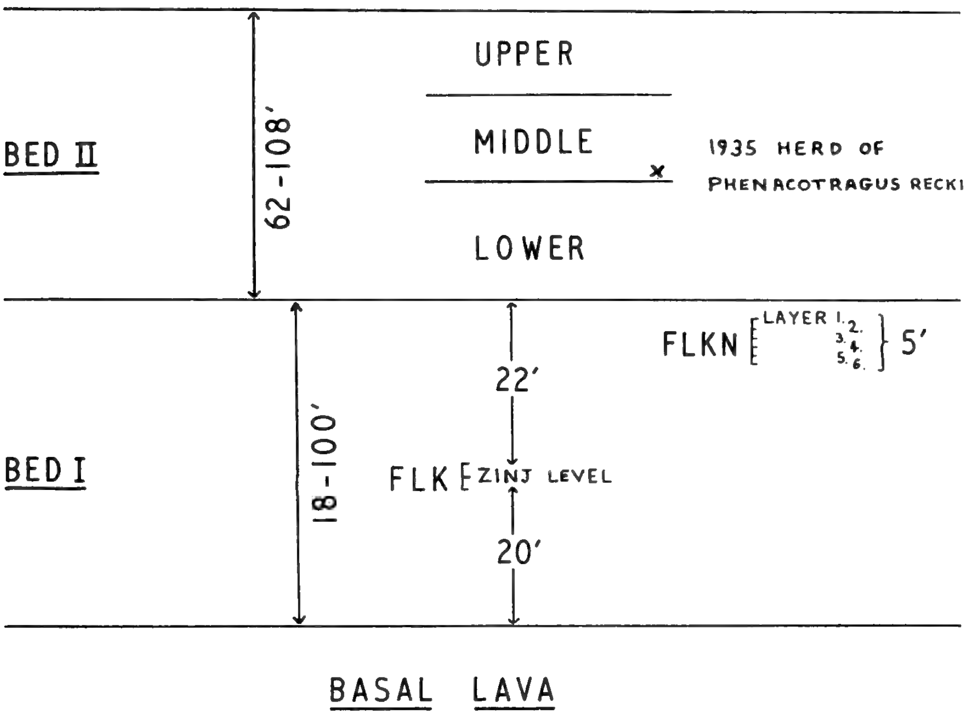


FIG. 1. Simplified diagram of Beds I and II, Olduvai Gorge.

Help and co-operation of various kinds have been received from numerous people, among them the following: in Oxford from Mr. H. K. Pusey my supervisor, Dr. A. J. Cain, and Dr. H. F. Lamprey; in Nairobi from Dr. L. S. B. Leakey and Mrs. S. C. Coryndon; at the British Museum (Natural History) from Dr. A. J. Sutcliffe, Dr. G. B. Corbet, Miss J. E. King and their staff; and during a short visit to Paris from Professor J. P. Lehman, Professor C. Arambourg, M. E. Heintz and staff of the Institut de Paléontologie. Dr. H. B. S. Cooke has kindly allowed me to see and refer to unpublished work on South African gazelline fossils. Most of the work was done in the Department of Zoology at Oxford on a research grant from the Department of Scientific and Industrial Research, and was submitted to the University as the greater part of a thesis.

II. GENERAL CONSIDERATIONS ON THE EVOLUTION OF GAZELLES

This paper deals with the tribe Antilopini, in which Simpson (1945) places six living genera other than *Gazella*. *Procapra* includes two or three Asian species which have frequently been assigned to *Gazella*. *Antidorcas* contains only one species, the well known springbok of South Africa, which does not range north of the Zambesi. *Litocranius* is the gerenuk of Somalia and East Africa characterized by its great shoulder height, an elongated neck, the long and massive occipital region of the skull, a brachyodont dentition and exceptionally shallow jaw rami. *Ammodorcas*, the dibatag, shares some characters with *Litocranius*, but its horns are forwardly curved from the base upwards, and it occurs only in restricted parts of Somalia. Little information is available on its ecology or on its ecological differences from *Litocranius*, with which it is sympatric and to which it is presumably closely related. Some notes on this rather mysterious animal are given by Meester (1960) and Schomber (1964). *Antilope* is the spiral horned blackbuck of India and *Aepyceros* is the impala which is very different from gazelles in face and coat coloration and in the shape of its horns. The females of most species of *Gazella* and of *Antidorcas* have horns, but in the other genera the females are hornless.

Among the fossil genera of Simpson's (1945) list, *Phenacotragus* is the one to which most attention will be given in this paper. *Dorcadoxa* from the Indian Pliocene consists of some frontlets and horn cores together with a " doubtfully referred " maxilla; Pilgrim (1939) thought these remains showed affinities with *Aepyceros* of East and South Africa. The other extinct genera, *Helicotragus*, *Protragelaphus*, *Gazellospira*, *Antilospira*, *Spirocerus* and *Dorcadoryx*, are all Eurasian spiral horned antelopes of Pliocene and Pleistocene age. Pilgrim looked upon them as having relationships with the living *Antilope*, and a review is given by Pilgrim & Schaub (1939).

The word " gazelle " in this paper is used as a noun or an adjective to refer only to the genera *Gazella* and *Procapra*, while " gazelline " refers to all the genera of Simpson's Antilopini including *Gazella* but excluding *Aepyceros*. The generic name " *Antidorcas* " or the English word " springbok " is used for the species *Antidorcas marsupialis*.

Definitions of the Antilopini and of *Gazella* have previously been given by Pilgrim (1939), Pilgrim & Hopwood (1928) and by Schlosser *in* Zittel (1925) as well as by earlier authors. Alterations and the addition of limb bone characters are proposed in the following definitions, and a definition of *Antidorcas marsupialis* is also given.

Tribe **ANTILOPINI** Simpson 1945

Small to medium sized antelopes with a moderately long face and braincase. Horn cores situated above the orbits or partly behind them. Horns of females smaller than in males or absent. There is a complicated suture between the frontals and parietal. The moderately long basioccipital does not narrow anteriorly except in some early forms. The face is little bent on the basicranial axis. The mastoid exposure of the periotic occupies a large surface area. An ethmoidal fissure is generally present between the nasal, maxillary, lachrymal and frontal bones. Most species have a small or medium sized preorbital fossa. Premaxillae are generally large and long. The infraorbital foramen lies above P^2 or P^3 when the skull is viewed with the tooth row in a horizontal position.

The molar teeth are brachydont in early forms but become hypsodont in many lineages. Basal pillars[1] on the inside of the upper molars and the outside of the lower molars disappear early in the evolution of the group. The enamel bordering the central cavities of the molar teeth shows little or no tendency towards a complicated pattern of folding. The premolars show relatively little advance in evolution towards molarization, and the central cavities of the upper ones are only rarely symmetrical; P_4 has an anteriorly closed medial wall only in some Asian *Gazella*.

The metapodials are long and their distal condyles have a large diameter. In the scapula the tuber scapulae comes well below the level of the glenoid facet in side view[2]. In the humerus there is no projection of the bone backwards and outwards behind the infraspinatus insertion as a posterior eminence[2]; the great tuberosity is more or less upright and not curved over the bicipital groove, the top of the medial tuberosity is not drawn upwards to a prominent point and the distal condyles have large diameters. There is considerable twisting of the axis of the radius[2] and the posterior edge of the top medial facet is often indented. The articular area for the scaphoid on the posterior surface of the radius is short and narrows rapidly. The posterior surface of the shaft of the metacarpal is only slightly concave.[3]

The gluteus accessorius insertion on to the femur is situated low and forwards on the great trochanter; the cnemial crest of the tibia does not grade smoothly into the shaft below but instead has a distinct lower end. On the metatarsal there is only a poorly shown groove running down the anterior surface, the naviculo-cuboid facet becomes smaller in comparison with the ectocuneiform facet during the history of the tribe, there is no ridge bounding the lateral extensor tendon medially at the

[1] Basal pillars lie between the anterior and posterior lobes of the molar teeth.

[2] Not in *Antilope*.

[3] Metacarpals assigned to *Gazella capricornis* in the British Museum (Natural History) have a deeply hollowed posterior surface.

top of the anterior surface, and the paired flanges towards the distal end of the anterior surface are prominent. A non-osteological character which is not useful in palaeontology is that the face often has a characteristic pattern of longitudinal dark and light striping. Most of the living species of Antilopini inhabit dry regions of the world and what observations there are suggest that they are facultative non-drinkers.

GAZELLA Blainville 1816

The horn cores have a sub-circular or elliptical cross section, their lateral surface is often flatter than the medial one and they have no torsion of their axes. In anterior view they are sub-parallel or divergent from one another; in lateral view they have a backward curvature which may take the form of a sudden, almost angular change of direction in some species. The females generally have horns which, when present, are set more obliquely than in males of the same species. Supraorbital foramina are situated in triangular-shaped depressions of the frontals—here called supraorbital pits—at the base of the horn pedicels. These pits are usually slightly on the medial side of the antero-posterior long axis of the pedicels. The level of the frontals between the horn bases is no higher or is only slightly higher than the level of the orbital rims. There are moderate to large sized auditory bullae. The pre-maxillae generally contact the sides of the nasals. The nasals have shortened in the evolution of the genus.

All living species have hypsodont teeth. The wall of the upper molars has three narrow vertical folds situated anteriorly, posteriorly and in the centre (parastyle, metastyle and mesostyle) as in many other Bovidae, but the two outwardly-bowed vertical swellings of the wall between the three styles are not prominent. The *pli caprin*[4] of the lower molars is less marked than in some Caprine genera. P_4 originally has a medial wall with an open anterior valley and two small posterior indentations between three pillars, but in most evolutionary lines the posterior valleys close up leaving only the anterior valley open.

The edge of the ectocuneiform facet at the top of the metatarsal is usually more upcurved in side view than in other genera.

There are typically two teats but sometimes four, inguinal glands, well-developed pedal glands, carpal glands and preorbital glands (Pocock 1910, 1918).

ANTIDORCAS Sundevall 1847

Antidorcas marsupialis (Zimmermann)

(Pls. 4A, 9B, C)

Description. The horn cores are little compressed, without flattening of the lateral surface. In anterior view they are nearly parallel at the base and then diverge outwards as they bend backwards. The horns of females are sometimes

[4] The pli caprin is a transverse expansion of the most anterior part of the lower molars separately from the main mass of the anterior lobe. It is best shown in some Caprine genera, also in *Gazellospira* and in lower teeth in the British Museum (Natural History) assigned to *Helicotragus* (Pilgrim & Hopwood 1928). In the present paper it will be called the goat fold.

more massive than in *Gazella*. Fewer individuals have a complicated frontals/parietal suture, and those with it have it less turned forwards in the centre. The supraorbital pits are small and the frontals between the horn bases are at a higher level than the orbital rims. The braincase is shortened ; the ethmoidal fissure very small or absent ; the preorbital fossa small ; the premaxillae reach the sides of the nasals ; and the nasals are long with very pronounced central anterior flanges. The auditory bullae are small ; the back of the basisphenoid is wide and its paired descending flanges originate at the back of the foramina ovales—more posteriorly than in *Gazella*. The palatal foramina may be set more posteriorly than in *Gazella*, and the hollow behind the maxillary flanges is deeper than in *Gazella*. The lower edge of the mandibular ramus rises rather steeply under the premolars from its great depth under the molars. The styles of the upper molars may be more pronounced than in *Gazella* ; the lower molars have straight medial walls with anterior inturnings ; the premolar row is very reduced. According to Pocock (1910, 1918) and Shortridge (1934) there are four teats, no inguinal glands, well developed pedal glands, no carpal glands, preorbital glands and a large dorsal gland on the back.

Fossil history of gazelles

In order to understand the gazelline remains of Olduvai, it is first necessary to consider briefly the history of gazelles and some of the characters used in their classification.

Gazella is first recorded in fossil form as the horn cores of *G. stehlini* in the European Upper Vindobonian ; according to Thenius (1951) it was a large species. *G. pregaudryi*, from Oued Hamman in Algeria, may also date from the upper part of the Miocene (Arambourg 1959). By Pontian (Lower Pliocene) times gazelles had become abundant in the faunas of Asia and the more southerly parts of Europe. Kurtén (1952) has clearly separated brachyodont and relatively hypsodont gazelles in China, but he did not consider how the Chinese species might be related to those of Europe. The best grounded Pontian species of Europe are :

1. *G. deperdita* from Cucuron, Mount Léberon and other sites, with slight lateral compression of its horn cores which are also slightly flattened on their lateral surface. Towards the tip they diverge outwards.

2. *G. capricornis* known principally from Pikermi in Attica. The horn cores are less compressed than in *G. deperdita* and have no flattening of the lateral surface. It may be noted now that flattening of the lateral surface of the horn core and degree of lateral compression are independent characters in gazelles ; it is not necessary that lateral compression be accompanied by a less convex lateral surface, and descriptive phrases such as " of circular (or non-circular) section " are not always clear.

3. *G. pilgrimi* (formerly *G. gaudryi*) from Samos has horn cores with a flattened lateral surface and a small degree of lateral compression but they differ from *G. deperdita* in the more regularly elliptical shape of their cross section and in being less blunt and not outwardly divergent at the tips. The premolar row is relatively shorter than in *G. capricornis*.

4. *G. mytilinii* is a larger species from Samos with distinctive lower teeth, if

those in the British Museum (Natural History) are correctly associated with the horn cores.

The best known gazelles of the later Pliocene are those from China, for example *G. blacki*.

G. borbonica from the Villafranchian (Lower Pleistocene) of Europe is about the size of the living East African *G. thomsoni* and very similar in appearance with its compressed horn core of nearly symmetrical cross section. The closest Pontian type of horn core would have been that of *G. pilgrimi* which is less compressed, but no relationship has been proved. The so-called *G. anglica* of the East Anglian Crags is probably the same species as *G. borbonica* and shows how gazelles had by then spread northwards. The contemporary *G. sinensis* of China is totally unlike *G. borbonica* and has large thick horn cores.

Pleistocene gazelles are common in Africa, and Arambourg (1957) recorded two extinct Upper Pleistocene species in North West Africa which are named *G. atlantica* and *G. tingitana*. The former has short, not very compressed horn cores which curve gently backwards and seem to stand between those of *G. deperdita* and *G. sinensis* in general appearance, although measurements show that they are actually less compressed than in either of these species. *G. tingitana* has very long, slender, curved horn cores without much resemblance to any other gazelle except just possibly to some of the horn cores from the Palestine Natufian levels assigned by Bate (1940) to *G. decora*, e.g. the horn core (M.16347) in the British Museum (Natural History). In South Africa one finds *G. wellsi*, a species to be considered in the next section. *G. gracilior* (Wells & Cooke 1956) is a small South African species with fairly steeply inserted horn cores which are less compressed than those of living African species. The name *G. praethomsoni* has been given to a horn core, a fragment of a mandible and a metatarsal from Omo in South Ethiopia (see Arambourg 1947). The horn core does not look unlike illustrations of *G. gracilior*, and is similarly less laterally compressed than in living species. Dietrich (1950) worked on gazelle material collected by Kohl Larsen's 1935 expedition to the Laetolil area near Olduvai; he separated teeth into three groups called *G. kohllarseni* (the largest), *G. janenschi* (the size of *G. thomsoni*), and *G. hennigi* (the smallest). Horn cores were found but appear in only one of the figures.

Fossil teeth referable to *Antidorcas* have been found in South Africa (Cooke 1963), but Arambourg's (1947) *Antidorcas* sp. from Omo does not appear to belong to this genus.

Characters used in the classification of gazelles

Gazelle horn cores thus show great variation of shape (compressed or not, flattened lateral surface or not), insertion (divergent or not in anterior view, rising steeply or obliquely from the frontals), and course (degree of backward curvature, outward divergence of the tips, sudden or gradual changes in course). Among the later types one could separate as two extremes the short, robust type of *G. sinensis* (with *G. atlantica* lying near to it), and the long, compressed, more nearly symmetrical type of *G. borbonica*. *G. pilgrimi*, *G. gracilior* and *G. praethomsoni* look more like *G.*

borbonica but are less compressed, while *G. capricornis* and *G. pregaudryi* are also quite unlike the *G. sinensis* type but are so little compressed as to be almost circular in cross section. The evolutionary relationship of these forms has not been worked out, nor has their history been brought into relationship with the evolutionary changes in the teeth. The most compressed horn cores appear later in the record, and presumably they and the *G. sinensis/atlantica* type could be traced back to an ancestral condition like *G. capricornis* or perhaps to a type intermediate between *G. capricornis* and *G. deperdita*. Despite their great intraspecific variability horn cores are undoubtedly the most useful fossil remains for classifying extinct gazelles, but one cannot assume that horn core similarity is a reliable indicator of phylogenetic relationship.

Various opinions have been held on the history of horns in female gazelles. The evidence is slender but it seems likely that they were already present in early forms as is supposed in *G. stehlini* (Thenius 1951) and that their disappearance is secondary. Hence *G. thomsoni* would be the most advanced living African gazelle for this character, for the females' horns are certainly small and most variable in direction and insertion as would be expected in an organ about to disappear. According to Pilgrim (1937) *G. lydekkeri* from the Dhok Pathan (Middle-Upper Pliocene) of India already had hornless females.

Concerning other skull characters of the genus, Pilgrim (1939) recognized that nasals are proportionately longer in the earlier species and this is borne out by measurement on a skull of *G. capricornis* in Paris in which the nasals were 6·34 cm long and 2·15 cm. wide. Taking width as a percentage of length gives a value of 34%, whereas estimates for the living *G. dorcas* and *G. thomsoni* have means of 46 and 58·5 respectively (Gentry 1964). The basioccipital of a *G. capricornis* skull in London (M.11440) and of a *G. deperdita* in Paris were short and relatively more narrow anteriorly than in living gazelles and were thus somewhat nearer to the condition of other early Boridae.

The character of the low level of the frontals between the bases of the horn is not different in the Pontian gazelles from those now living and is also found in the related genera *Oioceros*, *Helicotragus*, *Antilope*, *Litocranius* and *Ammodorcas*. The supraorbital pits of Pontian gazelles and of *Ammodorcas* and *Litocranius* are smaller than in living gazelle species but share with them the typical triangular shape around the foramina. The combination of triangular pits and low level frontals give this region of the skull its characteristic appearance in males of these genera (Plate 9A). *Antidorcas* on the other hand has frontals at a high level between the horn pedicels, and its small supraorbital pits, hardly distinguishable from the foramina they surround, are long ovals and not triangular in shape. It is thus likely that in Antilopini the size and shape of the supraorbital pits are at least partly correlated with the level of the frontals, if not entirely so.

The teeth of gazelles

In Pilgrim's opinion (1939 : 31) the teeth of the early gazelles are not far removed from the original Bovid condition, and the genus retains a relatively primitive tooth

structure throughout its history. However some evolutionary changes do occur, for instance: diminution of the basal pillars (in early gazelles these lie between the anterior and posterior lobes of the molar teeth on the inner side of the uppers and the outer side of the lowers), increasing hypsodonty, and an increasing depth of the mandibular ramus to house the longer teeth. The reason for the decline of the basal pillars (they may be retained in other groups such as the Reduncini and Bovini) is not easily understandable, but the other changes are obvious improvements of masticatory efficiency.

But these modifications within *Gazella* are not so pronounced as those which occur in other gazelline genera and in the closely related Caprinae. The list of possible changes is:

1. Little worn upper and lower molars come to possess transverse ridges across the anterior and posterior lobes. These ridges are seen on the dentine as well as on the enamel.
2. Accentuation of the styles on the outer walls of the upper molars.
3. A flattening of the outer walls of the upper molars between the styles. This may proceed to such an extent between the mesostyle and metastyle that the posterior outer surface becomes concave.

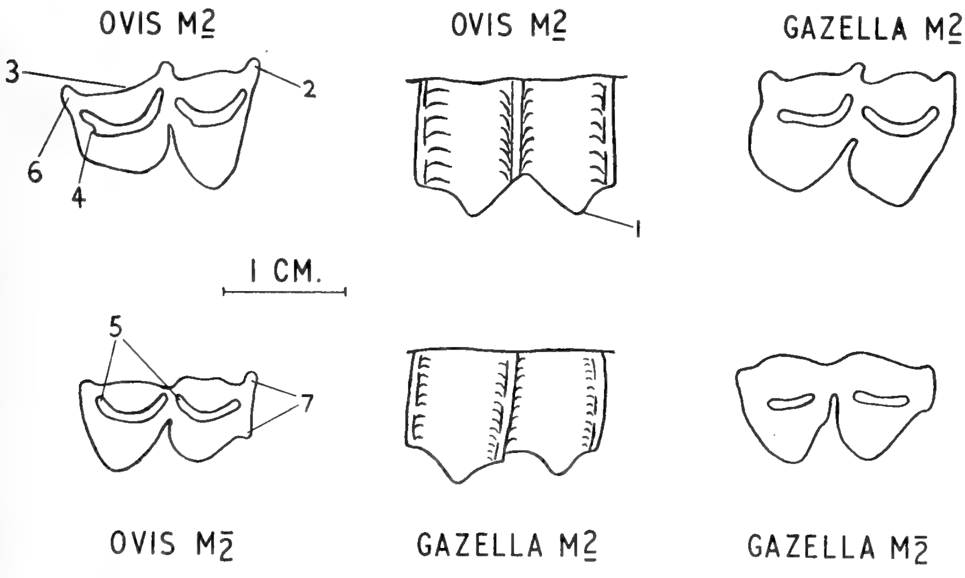


FIG. 2. Upper and lower molar teeth of a gazelle (*Gazella granti*) and a sheep (*Ovis aries*).

Occlusal views on the left and right, lateral views in the central column. The anterior side of every tooth is on the right; the lateral side of the upper molars is at the top and of the lower molars at the bottom. The numbers are those of the characters listed in the text. The shape of M^2 in *Ovis* with the anterior lobe being long and narrow and the posterior lobe short and wide is often found in Caprinae.

4. Increasingly complex course of the enamel wall around the central cavities of the anterior and posterior lobes of the upper molars: infoldings of the wall into the cavities appear.

5. The central cavities become longer and more curved, and they retain their symmetry better as they are worn down in life.

6. The metastyle of M^3 becomes a prominent flange.

7. Goat folds (see footnote on page 49) may develop on the lower molars.

8. The inner wall of P_4 is changed so as to make the tooth more like a molar.

9. The premolars may become so reduced that P^2 and P_2, or either, disappear.

Characters 1, 2, 3, often 4, 5, 6, 7, and 8, of the above list are easily examined on the teeth of *Ovis* or *Capra* (Text-fig. 2). Since the transverse ridges, 1, affect the dentine as well as the enamel, their presence may be attributed to changed occlusional movements, in gazelles the dentine of the lobes is often scooped out. The strengthened styles, 2, of the upper teeth are more resistant to the tops of the transverse ridges of the lower teeth and can be regarded as a correlated character. The concavity of the posterior outer wall in the upper molars, 3, probably helps to prevent the tip of its transverse ridge being chipped. The goat folds of the lower teeth, 7, avoid the consequences of the transverse ridges of the uppers acting across the divisions between the successive lower molars.

One can see these changes, and the molarization of P_4 as parts of an improved masticating mechanism. Varying combinations of all eight of these changes may evolve in Antilopine genera other than *Gazella*, and, according to Pilgrim (1939: 19), "alongside *Gazella* at every geological stage precocious Gazelline types are met with". When these changes are pronounced and accompanied by other skull alterations there is difficulty in assigning the genera to the Antilopinae or the Caprinae. The explanation for the different structure of gazelle and caprine teeth may be that they are adapted to feeding in different ways. Alternatively it is possible that selection in gazelles may not have acted primarily in favour of dental efficiency so much as in favour of cursorial improvements in the legs and the physiological mechanism for drought resistance. It was pointed out to me in discussion that if this were true, then the teeth of gazelles ought to be more variable than those of sheep and goats; such variability has yet to be proved.

It appears not to be wholly correct to describe such changes as adaptations to grazing. Nobody has ever suggested that the Caprinae are more fully grazing animals than the Antilopini, and it has been pointed out (Zeuner 1963) that within the Caprinae *Capra* is in nature more of a browsing animal while *Ovis musimon* at least is a more thoroughgoing grazer. None the less the detailed morphology of the teeth appears identical in the two genera. Then again very little is reliably known of the feeding habits of gazelles, although Brooks (1961) found that a high percentage of grass is taken by the East African *G. thomsoni*. However he also found that this species is a fastidious eater when the opportunity allows and that it prefers fresh shoots of grass where burning has occurred, and according to Lamprey (1963) *G. thomsoni* likes short grass previously grazed by other ungulates. In fact ecological

research might still show that gazelles are better described as mixed feeders with a tendency towards grazing, than as predominantly grazers.

Characteristics of P_4 have often been used in the classification of gazelles and their relatives, and some authors refer to primitive and advanced patterns of design. What seems to happen is that the inner wall of P_4 in the older fossil gazelles such as *G. capricornis* is indented by an anterior and two posterior valleys as can be seen in Text-fig. 3 in *Litocranius* which shows the same characters. In gazelle evolution there is a tendency for the more posterior pillars of the medial wall to coalesce, which leaves a more or less flat inner wall behind the surviving anterior valley. This condition is seen in the living species *G. thomsoni*. Among the Antilopini as a whole the possession of at least two valleys on the internal side of P_4 is a mark of early forms or can be seen as a primitive character in living species. But, as is usual with so many Bovid characters, there is much intraspecific variability and conclusions must be drawn with care. Some genera of Bovidae, but only the species *G. sinensis*, *G. gutturosa*, and *G. picticaudata* within *Gazella*, show a condition in which the anterior

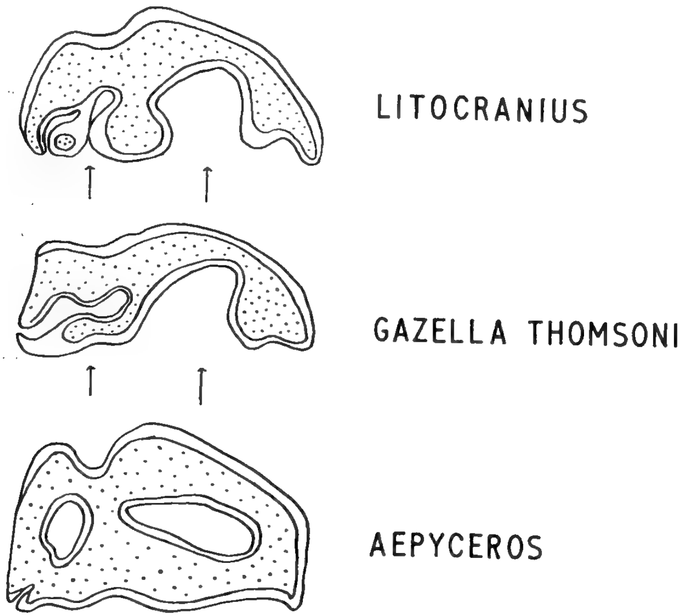


FIG. 3. Occlusal views of the left P^4 in three antelope genera. Not to scale.

The anterior side of each tooth is on the right and dots show where enamel has been worn away to expose dentine. *Litocranius* has anterior and posterior valleys on the medial side, shown by arrows; this is the condition found in early gazelles. In *Gazella thomsoni* the posterior valley has practically disappeared; this condition is found in later gazelles. It must also be noted that the posterior valley becomes more nearly closed up as individuals age, and that there is much intraspecific variation. In *Aepyceros* the anterior valley of the medial wall has closed up completely.

valley between metaconid and paraconid closes up as well as the posterior valley. The posterior part of the tooth shortens so that there is an almost entirely closed inner wall of P_4 formed from what would be the anterior part of the tooth in a gazelle. This character is clearly a move towards the molarization of P_4, and gazelles can be considered as not advanced.

The condition of P_4 in some of the species and genera mentioned in this paper is shown in the table :

	State of P_4	*Gazella* species	Other genera
I.	Posterior part of internal wall still open	*capricornis*	*Litocranius*, *Ammodorcas*
II.	Posterior part of internal wall closed or becoming closed	*pilgrimi*, *deperdita*, *dorcas*, *spekei*, *granti*, *rufifrons*, *thomsoni*	*Phenacotragus*, *Antidorcas*, *Antilope*
III.	Anterior part of internal wall closed	*gutturosa*, *sinensis*, *picticaudata*	All genera of Caprinae ; *Aepyceros*, *Alcelaphus*, *Damaliscus*

Among the gazelle species in category II the ones with the most nearly closed valley are probably *G. thomsoni* and *G. rufifrons*.

III. FOSSIL GAZELLINE SPECIES AT OLDUVAI

The remains of five or six gazelline species from the Olduvai beds will be described, although only two of them are well enough preserved to be referred to named species. The better represented ones show no apparent signs of relationship to the present day East African *Gazella thomsoni* or to *G. rufifrons* (a West African species similar to *G. thomsoni*). The most frequently occurring fossil species, *G. wellsi*, has some characters which are not entirely dissimilar from *G. dorcas*, but a far more likely phyletic relationship lies with the South African springbok.

Gazella wellsi Cooke

(Pls. 1, 2A, B)

1949 *Gazella wellsi* Cooke: 38, text-fig. 11.

MATERIAL

1960, FLK I, G13, 229	right horn core.
1960, ,, ,, 230	left horn core, presumably the same individual as 229.
1960, FLKN I, layer 5, 6334 . . .	crushed skull with horn cores and teeth. Plate IB.
1960, ,, ,, 1, 1307 . . .	crushed skull with right horn core. Plate 1A.
1960, ,, ,, 5, no no.	crushed skull with worn teeth.

1935, DK I, B.M. (N.H.) M.22360	right horn core.
1959, HWK II, 471	base of left horn core with top part of orbital rim.
1959, ,, 473	right horn core.
1959, ,, 568	left horn core.
1960, FLKN I, layer 3, 1152	left upper dentition. Pl. 1C.
1960, ,, ,, 3, 618	incomplete right upper dentition.
1960, ,, ,, 1–2–3, 871	right P^3–M^1.
1960, ,, no number	left M^1–M^3.
1960, ,, layer 1–2–3, no no.	left M^2–M^3.
1960, FLK I, Zinj. level G.323	right mandible. Pl. 2A.
1960, ,, ,, D.35	left mandible.
1960, ,, ,, G.294	right mandible. Pl. 2B.
1960, ,, ,, 492	left mandible.
1960, FLKN I, layer 1–2–3, 914	left mandible.
1960, ,, ,, 1–2–3, 935	right mandible.
1960, ,, ,, 1–2–3, 503	left mandible.

together with other fragments.

The size of the animal is about equal to that of the living Thomson's gazelle or slightly larger.

Horn cores

The horn core FLKN I, 1307 (Pl. 1A) which is probably from a male is robustly built. A short distance above the pedicel it bends backwards but does not diverge outwards, and then tapers quickly to a point. The medial surface is more rounded in section than the lateral surface and the horn core as a whole has little transverse compression. The diagram of the cross section (Text-fig. 7) also shows that while the anterior half is evenly rounded, posteriorly there is at least a tendency towards the development of a postero-lateral edge. Short and irregular longitudinal ridges and furrows are easily seen on the surface.

The two FLK I horn cores, nos. 229 and 230, are better preserved and more complete than the above specimen. They are less robust than 1307, have pronounced transverse ringing on the anterior surface, and are perhaps not quite so sharply bent backwards in their distal parts, but they have similar longitudinal ridges and furrows. Additional characters not observable on 1307 are that these horn cores do not rise very steeply from the frontals in lateral view, they are fairly strongly divergent from the base in anterior view (this character is to be distinguished from the outward bending of the distal parts alone which is seen in the *Phenacotragus* to be described later), the supraorbital foramina are set in small rather than large supraorbital pits and the frontals between the horn bases are at a higher level than the orbital rims.

The horn cores of the skull FLKN I, 6334 are as slenderly built as 229 and 230 and definitely less sharply bent back than 1307. The lateral surface is more noticeably

flattened than in 1307, the longitudinal furrows are not so deep, and faint transverse ridging can be felt on the lower parts of the anterior surface. On account of the slenderness and smoothness of its horn cores, 6334 is most satisfactorily interpreted as a female of the same species as its contemporary 1307 ; this leaves open the sex of the FLK horn cores from earlier in Bed I, the maleness of which would not have been questioned had 6334 not been found.

Horn cores comparable to 1307 have been commonly found at Olduvai since 1931, but they have nearly all been surface finds. F.939, F.940, F.944 and F.946 are surface finds from Bed I in 1941. In the British Museum (Natural History) M.14511, M.22363 and M.22479 are also surface finds from Bed I, whilst M.21456 is a surface find from Bed II and M.14563 from Bed IV. In addition there is a cranium, M.21463, which was a surface find from FLK II in 1935, and has retained both horn cores, complete supraorbital pits and much of its basioccipital. It is evident then that these horn cores have a long temporal distribution at Olduvai, since the 1960 specimens are undoubtedly from Bed I while M.21456 and M.14563 cannot be earlier than Bed II and Bed IV respectively.

M.22360, excavated from Bed I at site DK in 1935, is not a surface find and it deviates markedly from the 1960 horn cores in being narrow anteriorly and, less markedly, in having a more prominent postero-external edge. It agrees with the horn cores described above in the oblique insertion and outward divergence, and in the small supraorbital pit. The horn cores within many species of living gazelles show a considerable variability of shape, so it is most probable that M.22360 is conspecific with the 1960 horn cores. The impression given by all these horn cores is of one species, or at the most a superspecies, showing all the variation one might expect among its populations inhabiting the changing environment down the ages.

Upper teeth

The crushed skull FLKN I, 6334, provides the essential link between the horn cores and the upper teeth of this species. The teeth of this, as of most of the other specimens of upper teeth, are well worn. The youngest complete set is FLKN I, 1152 (Pl. 1C) which is in age state IX according to Brooks' usage (see Appendix 1), while the fragment FLKN I, 871 has two recently erupted premolars. In addition there are some comparatively unworn isolated molars from FLKN I, and FLK I.

There may be a difference from living African gazelles in the more prominent flange formed by the metastyle of M^3. When using this character it is essential to compare individuals of approximately the same age in different species, since the size of the metastyle increases in later life. Allowing for this age effect, one sees that *G. wellsi* may perhaps resemble Caprine genera and the Asian *Gazella picticaudata, G. gutturosa* and *G. subgutturosa* in this character rather than extant African gazelles. A number of isolated but unworn upper molars from FLKN I are probably assignable to this species ; the styles may be slightly more pronounced than in living gazelles but certainty is impossible. Apart from this and the development of the metastyle of M^3, the morphology of the teeth is like living gazelles.

The most startling feature of the upper dentition, however, is the extreme shortness

of the premolar row expressed as a percentage of the length of the molar row. The ratio can be determined on the skull 6334 and on the upper dentition 1152. Text-fig. 6 shows that the fossil premolar rows are as short as the shortest ones found in *G. thomsoni* which has the most reduced premolar row among living gazelle species in Africa, but it may be seen that the springbok has a still lower premolar/molar row ratio than the fossil, and it will be suggested that it is to *Antidorcas* and not to *Gazella* that *G. wellsi* may well be related. The actual statistics for the fossils and some living species were :

	Number Measured	Mean Value	Range	Standard Deviation
G. thomsoni	64	57·3	51–64	3·00
G. rufifrons	17	63·6	57–68	3·41
G. dorcas	31	63·4	58–69	3·17
Antidorcas marsupialis				
(with P^2)	9	47·8	46–52	1·85
(without P^2)	5	35·6	34–37	2·30

G. wellsi : c.50 ; 48 ; mean value : 49
FLKN I, 1662 : 49
Phenacotragus recki : c.56, 48, 59 ; mean value : 54·3
G. capricornis : 75, 74 ; mean value : 74·5

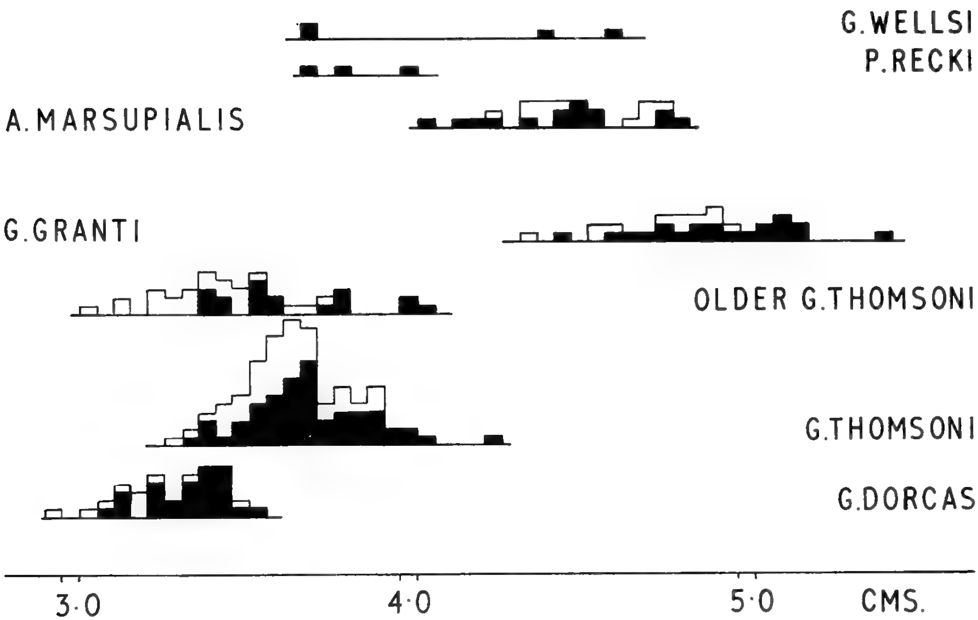
The confidence limits for the differences in mean values between the living gazelles were :

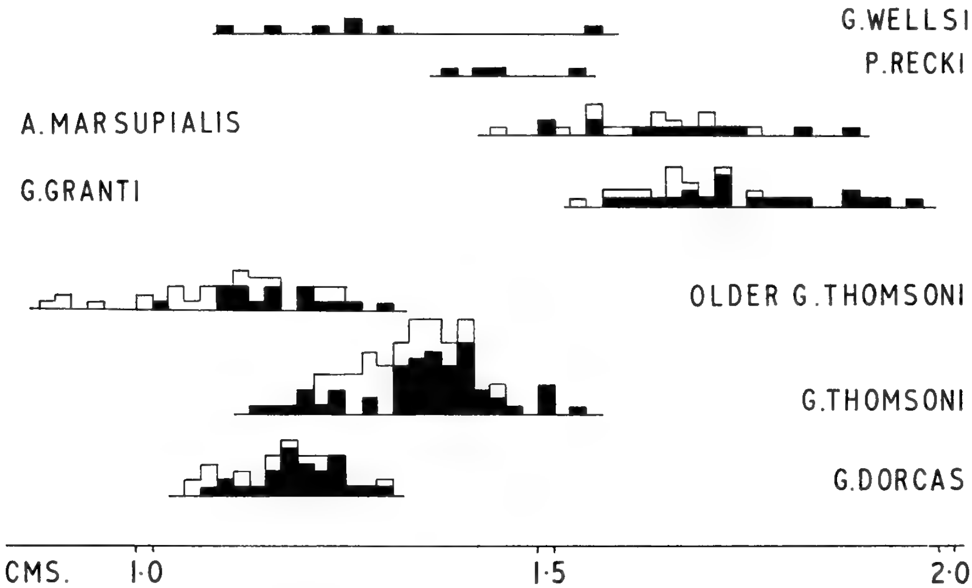
G. thomsoni–G. dorcas . . . . . 6·1 ± 1·32 with 93 degrees of freedom
G. thomsoni–G. rufifrons . . . . . 6·3 ± 1·68 with 79 degrees of freedom

The functional significance of the relative lengths of premolar and molar row is that longer molar rows are adaptive to grazing and perhaps to dust contamination of the grass eaten.

An upper dentition, FLKN I, layer 1, 1662 (Pl. 1C) is rather large but may belong to this species. Since the teeth are in age state X and since identification becomes more difficult with advancing age, there can be no certainty that it does not really belong to *Phenacotragus*. The styles on M^2 are slightly better developed than in the teeth of the other maxillae, but not so as to be beyond their possible range of variation. On the histogram of lengths of M^1–M^3 (Text-fig. 4), 1662 just comes within the possible size range of *G. wellsi* providing that the other fossils are all smaller than average size. On Text-fig. 6 the length of its premolar row is 49% of the length of the molar row. If 1662 is not *Phenacotragus*, then it might belong to a larger species closely related to *G. wellsi*. There is also the possibility of size changes within *G. wellsi* over periods of time, but more numerous remains are required for an analysis.

Finally, turning from tooth characters, it may be noted that the back of the maxillary bone in 1152 has a lesser slope as it rises towards the zygomatic arch than in living gazelles and that the right maxilla of 6334 shows the presence of a preorbital fossa as in living gazelles. 1959, HWK II, 471 shows that the orbital rims were wide.


G.WELLSI
P.RECKI
A.MARSUPIALIS
G.GRANTI
OLDER G.THOMSONI
G.THOMSONI
G.DORCAS
3·0
4·0
5·0
CMS.


G.WELLSI
P.RECKI
A.MARSUPIALIS
G.GRANTI
OLDER G.THOMSONI
G.THOMSONI
G.DORCAS
CMS.
1·0
1·5
2·0

Mandibles

Unfortunately there is no associated find of a lower jaw with an upper jaw or horn core. The mandibles listed above are, however, assigned to this species because their size is right and because the premolar rows are as short as in the upper teeth. Six of the ten pieces come from FLK, and all ten have worn teeth. The character of overriding interest is the extent to which P_2 has been reduced. It is very small in FLK I, G.154 and in FLKN I, 976 and could hardly have been larger in FLK I, D.65 and, finally, in FLK I, G.294 (Pl. 2B) it is altogether absent. The elimination of P_2 occurs in Alcelaphini, and in *Antidorcas, Pelea, Antilope, Saiga* and *Pantholops* and its absence is not always invariable. It is therefore noteworthy to find such an advanced condition so long ago as in the early part of Bed I at Olduvai. The probability is, in both the fossil species and in the springbok, that the tooth disappears some time in adult life. It has been well established (Dekeyser & Derivot 1956) that upper canine teeth can occasionally be found in very young Bovidae although never in adults, hence it would be surprising if P_2 were not present in very many individuals of the springbok and *G. wellsi*, at least as a vestige after eruption of the permanent premolars.

Most of the fossil specimens are crushed, but it can be seen (Pl. 2A) that the ramus is deep below the teeth, even anteriorly where it may perhaps exceed the depth usual in living *G. thomsoni* which, with other living species, is deeper than in Pontian gazelles. This character, taken in conjunction with the reduction and loss of P_2, suggests advanced grazing adaptations. The anterior edge of the ascending ramus is complete in FLK I, G.323 and it has a less abrupt slope than in *G. thomsoni*. This is in agreement with the slope of the back of the maxilla in FLKN I, 1152 and suggests that in these animals the tooth row as a whole lay rather forwards.

Comparisons

The first point to be made about this species is its obvious lack of relationship with the living gazelles of Africa, which I have considered in another paper (Gentry 1964). The shortness and sharp bending back of the distal parts of the horn cores and the

FIG. 4. Histogram of length of M^1–M^3.

The readings for the Recent species were taken on individuals in age states VIII and IX as explained in Appendix 1; the distribution for older *G. thomsoni* is for specimens in age state X and above, and shows the size decrease with advancing age. The reading on the extreme right of *G. wellsi* is FLKN I, 1662, including the metastyle flange of M^3; the reading to the left of it is of the same specimen excluding the flange. FLKN I, 1662 thus only just falls within the likely size range of the other two complete molar rows assigned to this species. It and FLKN 6334 are in age state X, while FLKN I, 1152 is in age state IX. Unblackened readings indicate females, blackened ones males in living species; all entries for fossils are blackened.

FIG. 5. Histogram of length of M^2.

Older *G. thomsoni* in age state X and above are shown separately as in Fig. 4; here there is a definite decrease in length with advancing age, caused by the growth of M^3. The reading on the right of *G. wellsi* is FLKN I, 1662. Unblackened readings indicate females, blackened ones males in living species; all readings for fossils are blackened.

slight transverse compression are not totally unlike the living *Gazella dama*, but in other respects there is no resemblance. The less reduced female horns are probably more primitive than in living species, but the teeth and lower jaws appear to be more specialized. On the whole it is less unlike *G. dorcas* than *G. thomsoni*; this is seen in such characters as the smaller supraorbital pits, the horn cores being bent backwards (although more sharply than in *G. dorcas*) and the comparative lack of transverse compression of the horn cores. (However, Text-fig. 7 shows that the widest part of the fossil horn core lies at a more anterior level than in *G. dorcas*.) These characters in the fossil are probably evidence for the view that *G. thomsoni* has evolved further from its ancestral condition, as far as they are concerned, rather than evidence for the fossil's relationship to *G. dorcas* in particular. The short premolar row is quite different from *G. dorcas*.

The species is not at all like *G. praethomsoni* from Omo (Arambourg 1947), which has a smaller horn core without a backward bend. *G. gazella praecursor* was described from Olduvai by Schwarz (1937). The type was not figured and so far as is known it was destroyed at Munich in 1944. The description speaks of hypsodont teeth and of horn cores being sharply bent back in their upper parts, but it also

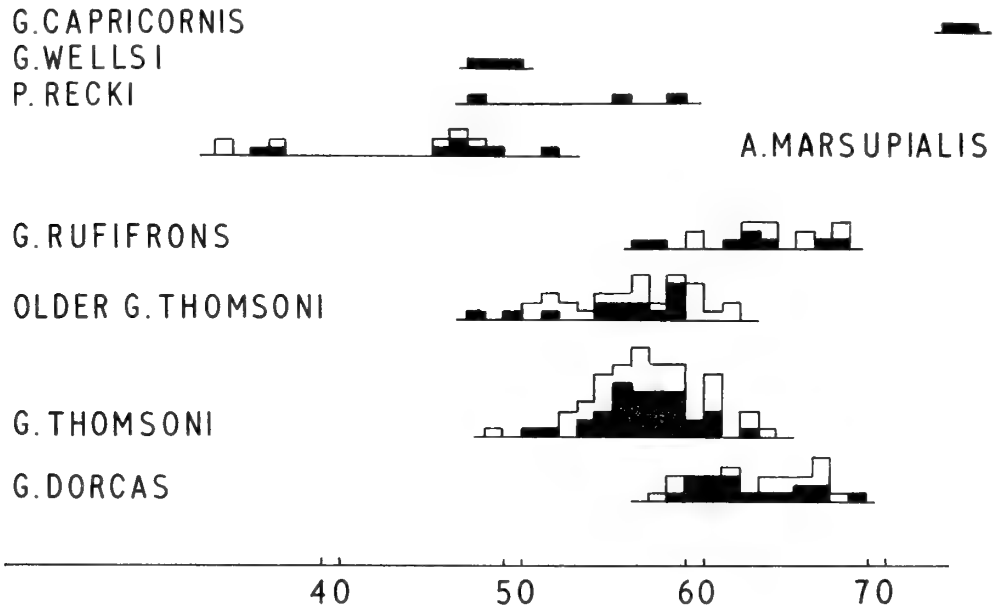


FIG. 6. Histogram of (length P^2–P^4/length M^1–M^3) × 100.

The group of *A. marsupialis* on the left are those without P^2, those on the right have retained it. Note the difference between *G. thomsoni* and *G. rufifrons*. *G. capricornis* is the main Pontian gazelle from Attica. Unblackened readings indicate females, blackened ones males in living species; all entries for fossils are blackened.

mentions that the upper parts of the horn cores diverged outwards and that they were laterally compressed with a basal index of about 65 or more. This does not sound like the present species. The horn cores of *G. atlantica* of the Algerian Upper

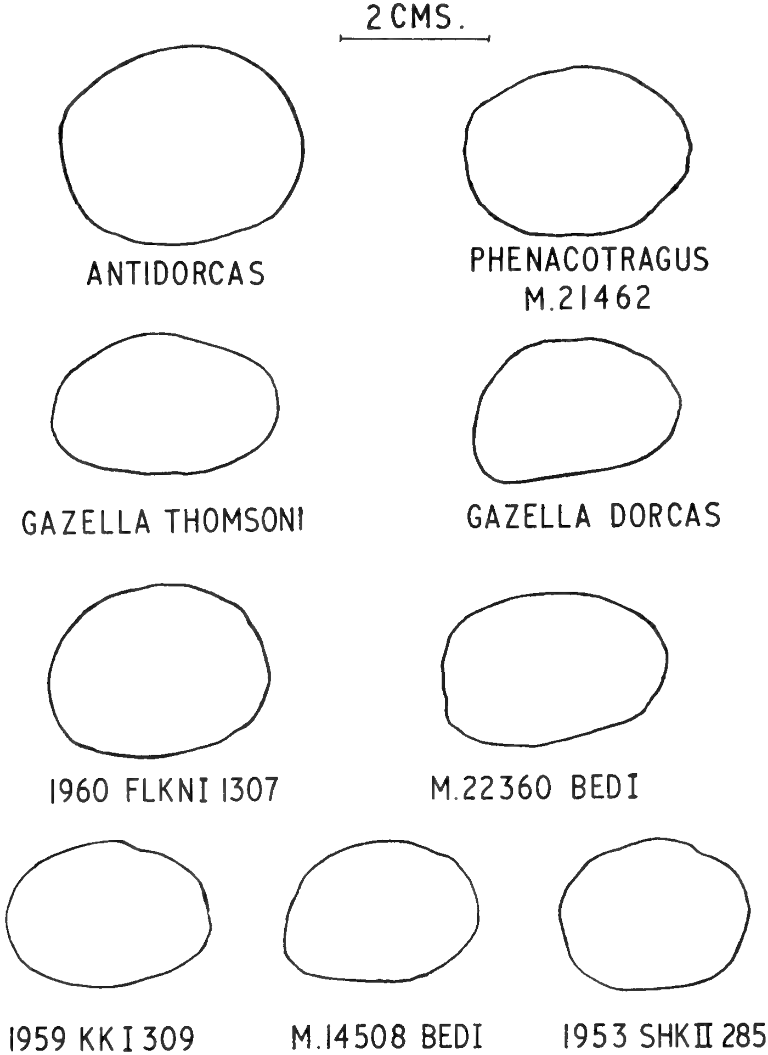


FIG. 7. Sections through gazelline horn cores.

The sections were taken at a distance above the pedicel equal to approximately half the antero-posterior diameter of the horn core in question. Thin wire was passed around the surface at right angles to the direction of the core, then carefully removed and its outline traced on paper. The lateral side of all the horn cores lies towards the bottom of the page, and the anterior side is on the right. The long axis of each section, here shown horizontally, is at a small angle to the mid-line of the skull.

Pleistocene are more like the Olduvai species, but they are larger, less sharply bent back and have more nearly triangular supraorbital pits.

The Olduvai species does appear to be conspecific with *Gazella wellsi* from South Africa. According to an unpublished paper by H. B. S. Cooke, this species possesses horn cores with pronounced transverse ringing which are sharply bent back near their base, little compressed, and without appreciable outward divergence in their upper parts. Its teeth are noteworthy for the shortness of their premolar rows and for hypsodonty. An undoubted female skull assigned to this species has the small horn cores characteristic of living gazelles, and is quite unlike the massive horn cores of the Olduvai skull 6334 which I believe to be of a female. Two factors may contribute to explaining this discrepancy. Firstly, the Olduvai female skull is likely to be from an older stratum than the South African one, which is from Bolt's Farm, a site belonging to the Swartkrans stage (see Cooke 1963 for a discussion of dating and correlation of African sites, and also for a record of South African sites from which *G. wellsi* is known). Secondly, the state of the female's horns may have varied among the populations of a wide ranging species. The extant Indian gazelle *G. bennetti* appeared to Ellerman & Morrison-Scott (1951) to be the eastern representative of *G. arabica* and they put both of them, along with other named groups, in the single species, *G. gazella* ; yet the horns of the *G. bennetti* females in the British Museum (Natural History) are more reduced than in *G. arabica*. This difference between the females of *G. bennetti* and *G. arabica* is admittedly less than that between the skull 6334 and the Bolt's Farm female.

Beyond the genus *Gazella*, it is *Antidorcas* which most resembles this Olduvai gazelle. In the springbok the horn cores are sharply bent back, those of the females are sometimes less reduced than in living gazelles, the supraorbital pits are small, and the level of the frontals between the horn bases is higher than the orbital rims, the premolar row is short and P_2 is often lost. In his unpublished work on the South African *G. wellsi*, Cooke also has noticed springbok-like traits, but not sufficient of them to justify a change of the generic name. These similarities will be taken up later and considered in a wider context.

Other gazelline skull and teeth remains from Olduvai

(A) Three horn cores 1959, KK I, 309 (Pl. 2C)
1959, HWK II, 472.
B.M. (N.H.) no. M.14512, Bed I, probably a surface find.

KK 309 and M.14512 are perhaps slightly smaller than *Gazella wellsi* while HWK 472 is smaller still and can reasonably be regarded as a female. All three are much compressed transversely and the cross section towards the tip shows a rounded anterior edge which narrows towards a fairly sharp posterior edge. The cross section in Text-fig. 7 is at a level comparable with the other sections but it is too low to show these features. The upper parts are sharply bent backwards but not appreciably outwards, and are like some horn cores of *Gazella wellsi*, e.g. 1960 FLKN I, 1307 (Pl. 1A), in this respect. They also have horizontal ridges on the lower parts of the anterior surface as in *G. wellsi*, but the shape of the cross section is different.

No gazelline fossils that I have seen from other sites are comparable to these horn cores, but it is impossible to say whether they are a separate species or a variety within *G. wellsi*.

(B) Six horn cores 1953, SHK II, 285 (Pl. 2C)
1955, BK II, 226
1959, KK II, 224
B.M. (N.H.) no. M.14507, Bed I, probably a surface find
B.M. (N.H.) no. M.22362 from FLK II (Pl. 7A)
1959, KK I, 310

They appear to belong to *Gazella*.

The first is the most complete and best preserved specimen. It is about equal to the size of a *G. thomsoni* male horn core and curves slightly backwards in its lower parts and slightly forwards nearer to its tip. The angle of insertion looks as if it is about equal to that of *G. thomsoni*. The lateral side is flattened, the medial side rounded and there is practically no transverse compression. The long axis of the cross section appears to be slightly less nearly parallel to the long axis of the skull than in *G. thomsoni* and the core diverges slightly more in anterior view. The pedicel

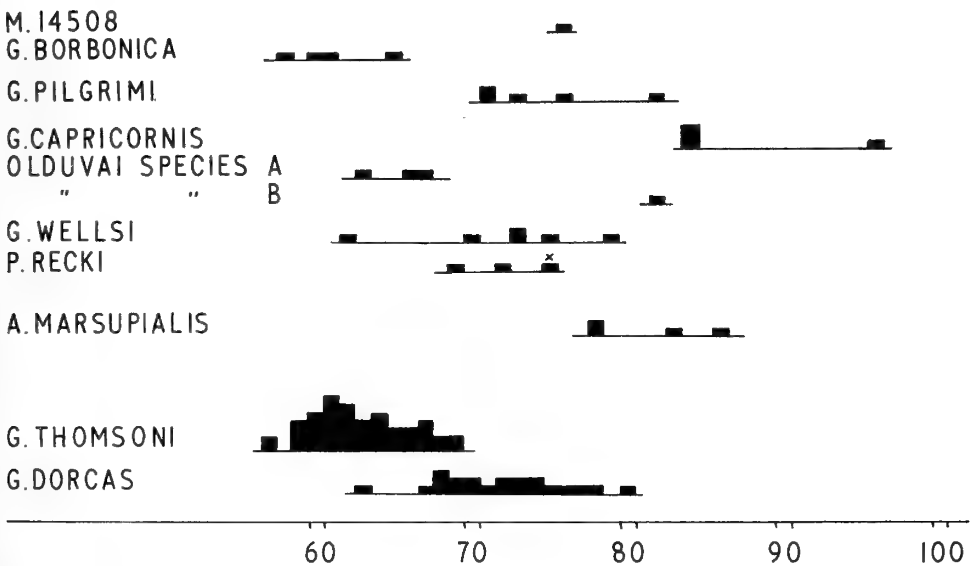


FIG. 8. Histogram of transverse diameter of horn pedicel as a percentage of longitudinal diameter. Only males have been measured in living species, but it is not certain that females have been excluded from among the fossils. The cross over one of the *Phenacotragus* readings marks M.21464, the supposed female. *G. capricornis* and *G. pilgrimi* are two Pontian species. *G. borbonica* is the Pleistocene species of Europe ; all except one of the readings were taken on English specimens—the so-called *G. anglica*.

is rather short in front (not in BK 226 or M.14507), consequently the height of the otherwise large supraorbital pit is reduced. The level of the frontals between the horn bases is about the same as that of the orbital rims. BK 226, which is from the left side, has a slight anticlockwise torsion from below upwards. Two very much thinner horn cores may be the females of this species—M.22362 from FLK II and more doubtfully 1959 KK I 310.

Neither the horn cores of group (A) or (B) are like any living gazelle.

(C) Three lower jaws, 1957, SHK II, 793, (Pl. 3A).
1952, BK II, 152
1955, Bed II, MLK surface find

These lower jaws may belong with either of the two sorts of horn cores in group (A) and (B) above or with neither of them, although an association with (B) may be more likely because its horn cores are almost entirely of Bed II origin. SHK 793 is the best preserved, with all its adult teeth present except P_2, which must have been destroyed after the animal's death. The length of the entire tooth row is about equal to that in *G. wellsi* but the premolar row is relatively longer. The length of the premolar row would have been about 2·3 cm. and the length of the molar row was 4·02 cm., thus the premolars' length was about 57% of that of the molars. The ramus is shallower below the teeth than in *G. wellsi* but the teeth do not look very brachyodont. It may have been not such a predominantly grazing gazelle as *G. wellsi*. The posterior half of the inner wall of P_4 is completely closed.

(D) One lower jaw—B.M. (N.H.) no. M.22379 (Pl. 3A).

This is an excellently preserved right mandible found in SHK, Bed II with the herd of *Phenacotragus recki* to be described later. It belonged to an adult, again about the size of *G. thomsoni*, and the teeth are not heavily worn. P_2 was present in life but has since dropped out. The posterior half of the inner wall of P_4 is completely closed. The depth of the ramus is as in the living *G. thomsoni*, and this separates it from the mandibles of group (C) and with less certainty from *G. wellsi*. The main point of interest is the long vertical ascending ramus ; this and the morphology of the teeth separate it from the *Phenacotragus* herd with which it was found.[5] The posterior half of the medial wall of P_4 is completely closed. It could be a later development from the *G. wellsi* stock of Bed I.

(E) Four lower jaws, 1960, FLKN I, 137, layers 1–2–3
1960, FLKN I, 1293, layer 1, (Pl. 3B)
1941, Bed I, F.109, surface find (Pl. 3B)
1941, Bed II, F.102, surface find,

together with some fragments of mandibles and isolated teeth.

There are several peculiarities in these lower jaws. The ascending ramus of 1293 rises high above the condyle for the squamosal articulation. Further, the horizontal ramus deepens rapidly as it passes back from beneath the premolars to the molars,

[5] A larger non-gazelline mandible was also found with this herd, and is now in the British Museum (Natural History) although unregistered.

and although the 1960 pieces are from sub-adult animals, F.109 is adult and still shows the same character. The pattern of the occlusal surface of the molars is not like that usual for gazelles, instead it somewhat resembles that of *Aepyceros*, *Antilope*, and the teeth at the British Museum (Natural History) assigned to *Gazella mytilinii* (M.4181–85). The medial walls bulge outwards from the body of the tooth between the styles, the walls of the central cavities are more evenly curved and each cavity is wider at its ends than in the middle. M_2 of FLKN 137 has a goat fold and the P_4 of F.102 has an open anterior valley on its internal wall; F.102 also shows a trace of the root cavity for P_2. These finds are not unlike Arambourg's (1947) *Antidorcas* sp., although that form is larger according to the measurements given, and lacks P_2. It is quite possible that these animals were not gazelline at all.

(F) One horn core B.M. (N.H.) no. M.14508, Bed I, probably a surface find (Pl. 3C).

There are quite a number of unidentifiable, presumably gazelline horn cores from Olduvai, and this one is selected for mention because it is about the size of *G. thomsoni* and does not look unlike that species at first sight, with its flattened lateral surface and the supraorbital foramen lying in a moderately sized pit. However, the extent of the lateral compression is no greater than in *G. dorcas* or *G. rufifrons* among living species. M.14508 will be considered further in the discussion of the Kanam West horn core in Appendix II.

IV. GAZELLINE LIMB BONES

A large proportion of the gazelline fossils at Olduvai are of limb bones, and it is of obvious interest to compare them with living species. To this end Recent limb bones of some antelopes were first compared among themselves and the findings were given in Gentry (in preparation) in which it was found that gazelles are not easily distinguished from one another or from the springbok. However the situation with the springbok might have been remedied had more than three specimens of it been available. *Litocranius* (the gerenuk) and *Ammodorcas* (the dibatag) had several distinctive characters, and *Aepyceros* was the least difficult genus to distinguish from gazelles. Differences of proportion between the species and genera were not considered in that paper but are immediately below.

Proportions of limb bones

Measurements were taken of the length and least thicknesses of the limb bones of three *G. dorcas*, six *G. thomsoni*, ten *G. granti*, five *Aepyceros* and two *Antidorcas*. Histograms were drawn of the ratios of least thickness to length of each limb bone and of the length ratios metacarpal/humerus, radius/humerus, metatarsal/femur and tibia/femur. These histograms (Text-figs. 9, 10) are an indication of cursorial adaptation in the various species.

In gazelles, but not so clearly, or not at all, in *Aepyceros*, the females have more slender bones than the males and relatively longer distal bones. The ranges of combined male and female readings for ratios in the front legs are usually greater than

those in the hind legs. Among the three gazelle species it is *G. granti*, the largest one, which has the thickest bones and its distal bones relatively shorter than in the other two species. The small *G. dorcas* is at the opposite extreme as would be expected, and in its back legs the ratios of metatarsal/femur and tibia/femur are very different from *G. thomsoni* and *G. granti*. The femur and humerus of *G. thomsoni* and the femur of *G. dorcas* are relatively thicker than in *G. granti*.

So far as can be reliably judged from two measurable specimens, the springbok is characterized by very long and slender metatarsals, long radii and long metacarpals.

The impala differs from the otheı genera and species in its relatively long radius and short metacarpal and perhaps also in a slightly longer and thicker tibia. These characters are presumably adaptive to jumping.

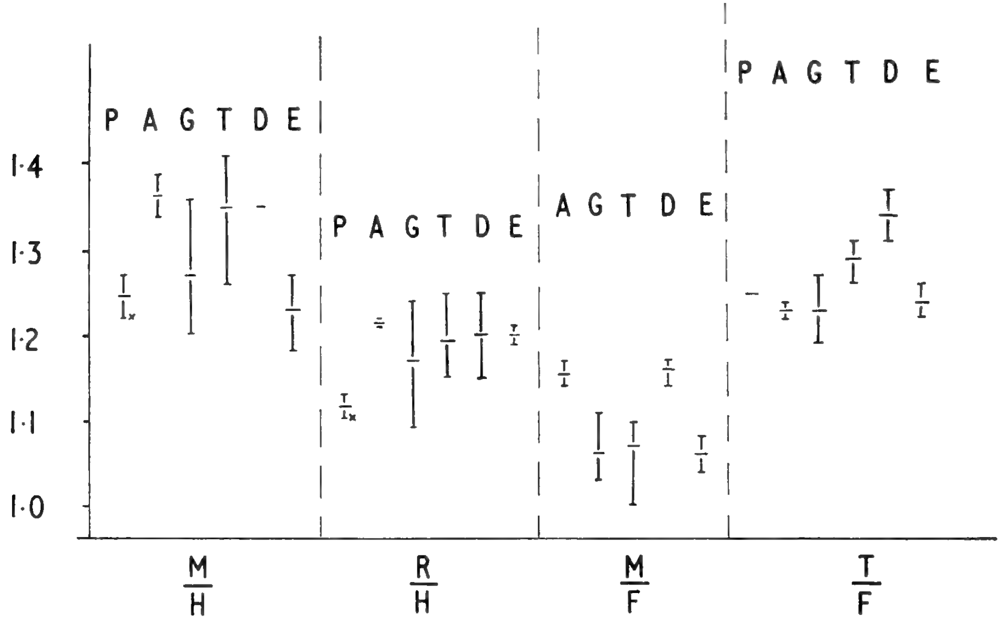


FIG. 9. Histogram of comparative lengths of limb bones.

$\frac{M}{H}$ = length of metacarpal/length of humerus; $\frac{R}{H}$ = length of radius/length of humerus;
$\frac{M}{F}$ = length of metatarsal/length of femur; $\frac{T}{F}$ = length of tibia/length of femur;

P = *Phenacotragus recki* A = *Antidorcas marsupialis*
G = *Gazella granti* T = *Gazella thomsoni*
D = *Gazella dorcas* E = *Aepyceros melampus*
W = 1960 fossils from Bed I.

The mean value and observed range are shown for each ratio in each species. Within *G. granti* and *G. thomsoni* the females have longer distal bones and thinner bones than the males, although this is not shown on the histograms. Crosses mark the fully adult individual of *Phenacotragus*.

Limb bones of fossil gazelline species from Olduvai

Femur

Only a few fragmentary remains of femora are available from the 1960 dig. FLKN I, layer 1, 1027 (Pl. 4A), is a proximal end with the top of the great trochanter missing. Its chief point of interest is a short, not very high, but sharp, vertical ridge on the anterior surface just below the lateral end of the articular head. In this position it forms the lateral boundary of the vastus medialis and intermedius origins. The ridge is only present in such a pronounced form in one of the eighteen femora of living gazelles available for comparison although there was a tendency towards it in some *G. granti*; it was also seen in a male springbok femur at the University Museum in Oxford in which it was less sharp, but in no other genus. The neck supporting the articular head of the fossil can be seen in medial view to be as thin as in living species. The gluteus accessorius insertion lies forwards. The hollow between the great trochanter and the articular head is not so deep in anterior view as in living species. The size of the fossil is of an animal intermediate between *G. granti* and *G. thomsoni*. FLK I, K, upper levels is a left proximal end with the hollow between the articular head and the great trochanter rather shallow and the medial part of the articular head projecting somewhat forwards from its neck,

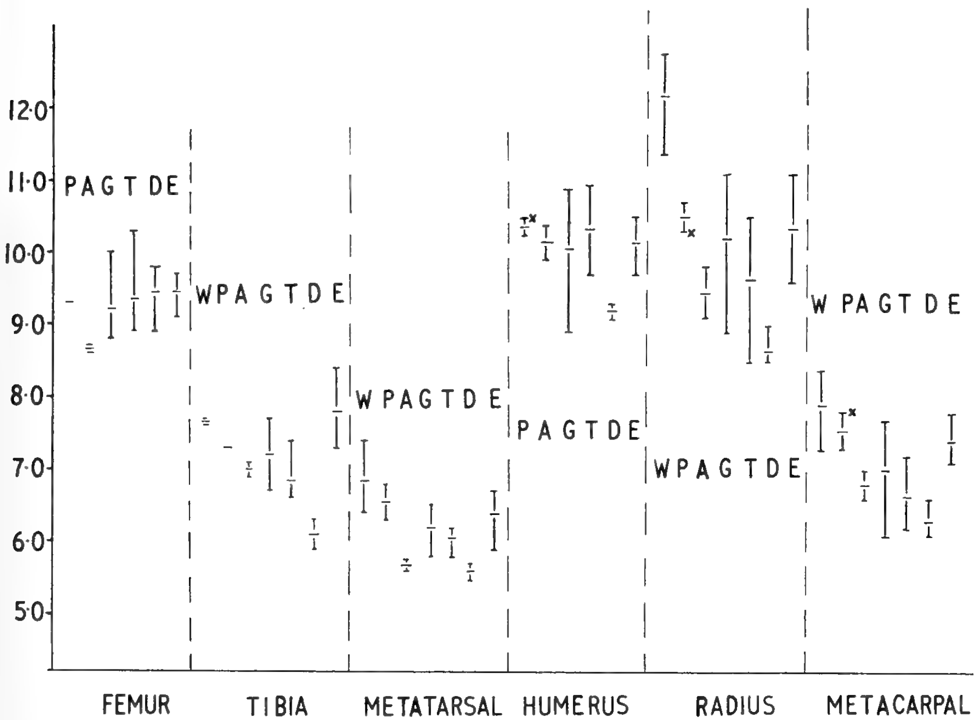


FIG. 10. Histogram of least thicknesses of limb bones. Initials as in Text-fig. 9.

thereby showing a puzzling resemblance to reedbucks in one character and to sheep and goats in the other. FLKN I, layer 1–2–3, 28 is a shaft with distal end. If one looks at it in ventral view, the part behind the origin of the lateral femoro-tibial ligament looks slightly more convex than in living gazelles. This difference is slight, and otherwise the fossil bone and Recent bones are indistinguishable. The top of the lateral condyle is flat as in *G. thomsoni*, and the size is about that of *G. thomsoni*. FLK I, F/15, 150 is a similar distal end.

A number of other articular heads are quite likely to be gazelline, among them FLKN I 402 and FLKN I 6242.

Tibia

There are more tibiae than femora from the 1960 Olduvai excavations:

complete bones	FLK I, F.161 (Pl. 4B)
	FLKN I, layer 1, 1246 and 1284 (probably the same individual)
almost complete	FLKN I, layer 2–3, 685
	FLKN I, layer 1–2–3, 157
proximal ends	FLKN I, layer 2–3, 658
	FLKN I, layer 1–2–3, 492 (only the back part of the articular surfaces)
distal ends	FLK I, 257
	FLK I, 510[6]
	FLK I, 664
	FLKN I, layer 1, 1564
	,, 2–3, 651
	FLKN I, layer 3, 1157, 6087, 6183, 6270, 6290
	,, 5, 1818, 5189
	,, 1–2–3, 81, 931

The tibiae seem to belong to an animal about the size of *G. thomsoni*; the top articular surface is about the size of that species but the length is less. The thickness of some of them is greater than in *G. thomsoni*; of others about the same. The only two measurable ones are so thick as to be outside the range of *G. thomsoni* (see Text-fig. 10). No good difference is discernible between the FLK and the FLKN remains, but both show some differences from living gazelles. Towards the proximal end, the posterior surface is less flattened and more convex and the subsequent raising of the ridges for the long digital flexor origin gives the bone an appearance reminiscent of Reduncini. The long digital flexor ridge lies more closely to the medial edge of the posterior side than in living gazelles; a condition almost like that of the impala, *Aepyceros*. The lateral surface of the cnemial crest is noticeably concave, perhaps more than in *G. thomsoni*. The long axis is curved

[6] This is from level G.15, together with another unnumbered distal end. Three more unnumbered distal ends are from FLK I level G.13; all other FLK I fossils throughout this paper are from the Zinj level.

forward at the top and bottom of the bone more than in any living gazelline species. It seems very unlikely that distortion could be responsible for this in so many specimens. At the distal end the medial malleolus is shorter and its posterior wall more diagonal than in living species. Also at the distal end the level of the anterior top edge of the fibula bone looks as if it is less high than in living species, but this is not a certain difference, and it is too easy to anticipate it from the character of the medial malleolus on the opposite side. In other characters the fossils agree with living gazelles.

M.14618 is a proximal end from Bed I, and is apparently identical with the above remains. It shares with FLK I, F.161 a greater slope of the surface for the insertion of the ligament from the patella at the top of the cnemial crest than in the only complete top end from FLKN I—number 1284. But this is probably not beyond the range of intraspecific variation. 1957, LK I (surface find) 891 also agrees with the distal ends. Alcelaphine distal ends are almost indistinguishable from those of gazelline genera, and there are a number of indeterminate specimens (e.g. M.22349–53). The absence of comparably large gazelline-like limb bones other than tibiae decreases the likelihood of these ones belonging to the Antilopini.

Metatarsal

A number of fairly complete metatarsals are available from the 1960 dig :

complete	FLK I, C.1227, F.219
	FLKN I, layer 1–2–3, 3, 199, 464, 530
	,, 3, 6198
	,, 5, 1454, 1758, 5194
Proximal ends	FLK I, C.1054, G.358
	FLKN I, layer 1–2–3, 527
	,, 2–3, 671
distal ends	FLK I, D.124 + D.26 (two pieces of the same bone)
	FLKN I, layer 3, 6184
	,, 2–3, 740
	? , 758
	layer 1–2–3, no number
	,, 1, no number.

They are shorter than in *G. thomsoni* but thicker ; the distal end FLKN I 740 has the least transverse thickness. Those from FLK are slightly larger than those from FLKN. They differ from living species in that the naviculo-cuboid facet is slightly larger in comparison with the facet for the ectocuneiform. The naviculo-cuboid facet is not actually larger than the ectocuneiform facet, only less reduced than in living species. This can be seen in the histogram on Text-fig. 11. The difference between these fossils and *G. granti* for linear measurements across the two facets was $5{\cdot}5 \pm 4{\cdot}73$ with 16 degrees of freedom, a small difference with wide confidence limits. However it probably is a true difference and it is likely that there is a tendency to reduce the area of the naviculo-cuboid facet in gazelline evolution.

An alternative measurement from the front to the outermost point of the rear edge of the naviculo-cuboid facet, instead of to its central point, when compared with the readings for the ectocuneiform facet gave a non-significant difference from *G. granti*. The front of the top articular surface is less upcurved than in living species. There are no other sure differences from living gazelles.

FLKN I, layer 1–2–3, 613 is a distal end from the 1960 excavations which is too large to belong to the above species. It is about the size of a small *G. granti* and is definitely gazelline by the prominent anterior flanges above the condyles. FLKN I, layer 3, 5000 is a complete metatarsal which could conceivably belong with 613 or with most of the metatarsals considered above. However it is difficult to visualize such a slender bone as 740 in the same species, so 5000 may provisionally be placed with 613. As far as size is concerned the proximal femoral end FLKN I 1027 would go with these two metatarsals. There is no other reason why the femur and metatarsals should be put together, but it is instructive to find out the minimum number of species to which the fossil limb bones may be assigned.

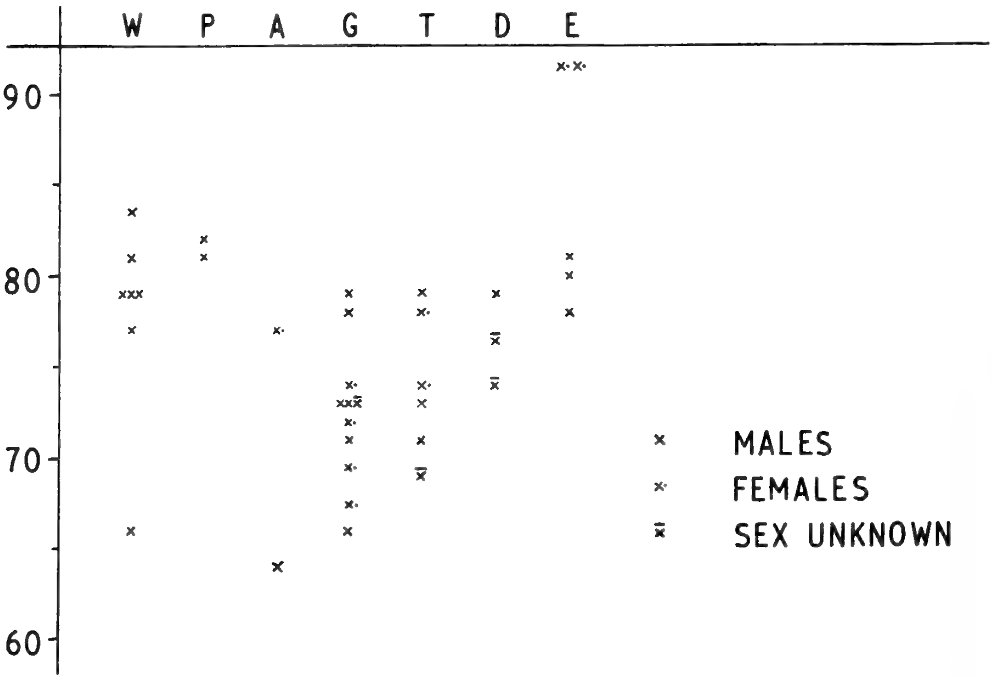


FIG. 11. Histogram of length of the metatarsal's naviculo-cuboid facet/length of its ectocuneiform facet. $\times 100$. The measurement of the naviculo-cuboid facet was taken from its most anterior point at the junction with the ectocuneiform facet to the centre of its rear edge. The measurement of the ectocuneiform facet was from the anterior point of the junction with the naviculo-cuboid facet to the point where its rear and medial edges meet. The initials are as on Fig. 9. *Aepyceros* probably has a relatively larger naviculo-cuboid facet than in gazelles, as the 1960 fossils from Bed I might also have done.

A proximal end 1959, KK I, 248 is about the same size as the majority of the 1960 bones but shows a number of clear cut morphological differences. The posterior hollow at the top is shallow and without a foramen; there is a small hump on the edge of the posterior side lateral to where the foramen would have been if it were present. The groove down the anterior surface is better shown than in other fossils and there is a ridge medial to the lateral extensor tendon at the top of the anterior surface. This proximal end could easily be from the same individual as a distal metatarsal end KK 249 which has the gazelline prominent flanges above the distal condyles. If KK 248 is gazelline it is from a peculiar species, if it is not gazelline its affinities are very obscure. The combination of shallow posterior hollow, anterior groove and the ridge at the top of the anterior surface is also found in the Caprinae.

Astragalus

FLKN I, layer 1–2–3, 10, 577
,, 2–3, 708
,, (?), 1564
and two from FLKN I without numbers.

They are about the size of *G. thomsoni* and differ from those of living gazelles only in that the lower part of the lateral side is more deeply excavated. FLKN I, trial trench, layers 1–2–3, no number, is about the size of a springbok astragalus and thus perhaps too large to belong to the above species. It differs further in having a less deeply excavated lower lateral side.

Naviculo-cuboid

FLKN I, layer 1–2–3, 15, 81, 924 (and one without a number, from layer 3)

They are about the same size as in *G. thomsoni* and differ from living species of gazelles only in having the posterior wall project less when it is seen in medial view. 1959, HWK II, 5 could belong to this group. FLKN I, 1564 has its posterior wall projecting so little that it may be a separate species from the other four above.

Scapula

FLK I, D.177
FLKN I, layer 3, 1358, 1359, 1740, 6076
FLKN I, layer 1–2–3, 820

Only the stems have been preserved in 1740 and 6076. They do not differ from the scapulae of living gazelles except perhaps in a less concave surface for the origin of the teres minor and long head of the triceps. 1959, KK I, 478 probably also belongs here. An unnumbered stem from FLKN I and a stem FLKN I, layer 1, 1467 are separable from the others by being larger and having flatter medial sides. They may be of a different species.

Humerus

Proximal ends	FLKN I, trial trench, layer 3, fall
	FLKN I, layer 1, 1307, and one without a number
Shaft	FLKN I, layer 1, 1593
distal ends	FLK I, C.1181 (fits radius C.1176 and olecranon C.1177)
	FLK I, B.135 (fits radius B.136)
	FLKN I, layer 1, 1346
	FLKN I, layer 1, 1418, 1730
	FLKN I, layer 1–2–3, 54, 71, 381, 587, 633, 654
	FLKN I, layer 3, 6092
	FLKN I, layer 1–2–3, 9031
	FLKN I, layer 5, 1207, 1813
	FLKN I, one with no number from layer 1

No complete gazelline humerus was excavated in 1960. The most nearly complete specimen with a proximal end present is labelled FLKN I, trial trench, layer 3, fall. It would probably have been slightly shorter than in the living *G. thomsoni* but no less thick. Although the medial tuberosity is missing, the top of the bicipital groove may be at a lower level relative to the front of the articular head than is usual in living gazelles. In its other characters this humerus is just like that of a living gazelle. The two other fragmentary proximal ends and the shaft cannot be separated from the above piece.

There are a large number of distal ends of humeri ranging in size from being intermediate between *G. granti* and *G. thomsoni* (e.g. FLK I, C.1181) down to the size of a rather small *G. thomsoni* (e.g. FLKN I, 1730). Apart from the size range there are also morphological differences. Thus FLKN I, layer 1, no number and FLKN I, 1207 have relatively less high medial condyles, and three other distal ends (FLKN I, 1813, 6092, and 9031) have the top of the articular facet extending less far into the coronoid fossa on the anterior surface which has the effect of lowering the height of the medial condyle. But in the rest of the 1960 fossils, as well as in living gazelles, the humerus has a relatively high medial condyle and the top of the articular facet extends far into the coronoid fossa. It is reasonably certain that more than one species is present among the 1960 humeri but classifying the intermediates is impossible.

Radius

Complete	FLK I, D.100
	FLKN I, layer 1–2–3, 70, 50 (same individual as 70?)
	FLKN I, layer 2–3, 666, 682, 730, and one without a number from layer 5

proximal ends FLK I, B.136 (fits humerus B.135)
FLK I, C.1176 + C.1177 (fits humerus C.1181)
FLKN I, layer 1, 1480
layer 3, 6809
layer 1–2–3, 269 and one with no number
layer 5, 1448 and 1816

distal ends FLKN I, layer 3, 6105

The 1960 radii are about the same length as in *G. thomsoni* or slightly less but they are more massive than in any living gazelle, as can be seen in Pl. 4C. They differ from living gazelles as follows. The antero-medial corner of the medial facet on the top surface has as sharp an angle as in *G. thomsoni* and *G. rufifrons*; such a corner occurs also in *Aepyceros*, *Litocranius*, *Ammodorcas*, and *Antidorcas* but is not well seen in other living *Gazella* species. In some of the fossils the side edge of the medial facet is also angled, and this can be clearly seen only in *G. thomsoni* among living species. The medial facet is but little indented along its posterior edge; this is like *G. thomsoni*, *G. dorcas* and *Aepyceros* among living forms, whereas *G. granti*, *G. spekei*, *Antidorcas*, *Ammodorcas* and *Litocranius* are indented. The lateral facet is as flattened as in two of the three *Antidorcas* skeletons and *Aepyceros*, but it is not so long as in *Aepyceros*. The tubercle for the lateral humero-radial ligament projects less far and is slightly lower on the shaft than in living gazelles. There is perhaps less torsion of the stem, but this is rather uncertain. At the distal end the medial edge of the scaphoid facet projects further ventrally than in living gazelles; in this it is perhaps like the impala and the springbok. Apart from the 1960 radii, the proximal ends 1959 KK I 289, 1959 MK I 36 and 1959 HWK II 417 and the distal ends 1959 KK I 262, 1959 HWK II 416 and 1953 BK II Extension 42 may best be put in this group.

Four radii excavated in 1960—FLKN I, layer 1, 1010, 1300[7], 1605 and FLKN I, layer 3, 6049—are smaller than the group described above and have medial facets which are more compressed antero-posteriorly. These radii could be put with the humeri with rather low distal medial condyles since one would expect low humeral condyles to go with short medial facets on the radii. From the point of view of minimum number of species the naviculo-cuboid FLKN I 1564 could join these fore-limb bones.

Metacarpal

Complete bones FLK I, D.133
FLKN I, layer 1, 1273, 1306
layer 3, 6050
layer 2–3, 762, 764
layer 5, 1450

[7] Probably the same individual as 1010.

Proximal ends	FLK I, D.33–36	
	FLKN I, layer 1, 1276, 1481	
		layer 3, 5161 + 5164, 6100, 6194, 6255
		layer 1–2–3, 840
Distal ends	FLKN I, 1482	

Most of the metacarpals are shorter than those of *G. thomsoni* but more massively built. The complete one from FLK is slightly larger than those from FLKN I. They differ from living gazelles in the following characters. There is a better developed anterior proximal foramen, some of them have the posterior edge of the top articular surface indented, or not so completely continuous as in living species, an angled antero-medial corner of the magnum-trapezoid facet is poorly present as in *Gazella* except *G. granti*, and the angled corner on the antero-lateral side of the unciform facet is intermediate between its condition in *Litocranius* and in the living species of *Gazella*. The fossils agree with living gazelles in the lack of a concavity down the posterior side of the shaft.

The five pieces FLK I D.33–36, FLKN I 1481, 6050, 6100, and 6255 could be separated from the rest of those in the above list on the grounds that the posterior indentation of the top articular surface and the angled corner on the unciform facet are better developed. If this separation should be valid, the most likely assignment of these metacarpals would be with the humeri with small medial condyles and radii with antero-posteriorly compressed medial facets. But on the present evidence such a separation is doubtful.

FLKN I, layer 2–3, 655 is a complete metacarpal which differs from the bones above (but is probably not a separate species) in having a sharper corner of the antero-medial edge of the magnum-trapezoid facet, in being slightly more hollowed towards the top of the posterior side, in the shaft being more transversely compressed, in having large shallow hollows above the distal condyles on the posterior side and in the spaces for the tops of the phalanges above the condyles anteriorly being more restricted.

The distal ends FLK I D.120 and FLKN I, layer 1, 966 are larger than any of the previously mentioned metacarpals. They might be a separate species. The flanges of the condyles project less strongly from the medial facets of the condyles than in the above groups. The distal end FLKN I 1443 has hardly larger dimensions than the first group but may be placed with D.120 and 996.

Conclusions

The question arises of whether to allocate the main mass of the fossil limb bones to *G. wellsi* or not. There is no definitely proved association with the skull parts and only the radii, metacarpals and, more doubtfully, the naviculo-cuboids are distinguishable from those of *Phenacotragus recki* to be described next. While it is probable that the most numerous gazelline limb bones at a site go with the most numerous remains of skulls and teeth, the more prudent course is to say that the limb bones probably are those of *G. wellsi* with which they agree in size, despite a

few Bed I remains which appear to be *Phenacotragus*. They have a surprising number of differences from living gazelles. These differences and their massive proportions are extra evidence for the view that the gazelline fauna of Olduvai Bed I is markedly different from that now existing in Africa. The limb bones will henceforth be referred to as the 1960 fossils.

Several of the larger bones may tentatively be put together ; these are the scapula 1467 from layer 1 of FLKN I and the unnumbered companion piece, the femur 1027 from layer 1, the metatarsals 613 from layer 1–2–3 and 5000 from layer 3, the metacarpals 996 from layer 1, 1443 from layer 5, 120 from site FLK I, and an unnumbered astragalus. They may be from a separate larger gazelline species, or they may be evidence of size changes within *G. wellsi* or *Phenacotragus*.

The table below relates the fossil remains of skulls and teeth to those of limb bones as far as is possible.

		Horn Cores	Jaws and Teeth	Limb Bones	Main Occurrences
I.	*Phenacotragus recki*		As listed later		Bed II and probably also I.
II.	*Gazella wellsi*		As previously listed		Bed I, probably later also.
III.	Larger gazelline species	none	maxilla 1662?	femur 1027 etc., as in last paragraph.	Bed I.
IV.	Gazelline species	group (A)	mandibles (C) or (D). Mainly upper part of Bed II	humeri with low medial condyles, radii with short medial facets, metatarsals KK I, 248 and 249.	Bed I and lower part of II for horn cores.
V.	*Gazella* species	group (B)	mandibles (C) or (D). Mainly upper part of Bed II.	as for IV above?	Upper Bed II for horn cores.
VI.	*Gazella* species	M.14508	mandibles (E)	as for IV above?	Beds I and II for mandibles.

Site HWK II is in the lower part of Bed II ;
sites BK II and SHK II in the upper part.

It would be surprising if the mandibles (E) were in fact conspecific with the horn core M.14508, but the table gives a minimum number of species. The question of how many species occurred together at any one time in the Olduvai region will be answered as stratigraphical details become more precisely known.

V. NEW MATERIAL OF *PHENACOTRAGUS*

Phenacotragus recki (Schwarz)

(Pls. 5–8)

1932 *Adenota recki* Schwarz : 1, text-figs. 1, 2.
1937 *Phenacotragus recki* (Schwarz) Schwarz : 53, pl. 1, fig. 1.

Schwarz (1937) described this species more fully than in 1932 mainly on a skull excavated from Olduvai Gorge in 1913 ; its stratigraphical provenance within the

gorge is unknown. A cast of the type skull is in the Department of Palaeontology, British Museum (Natural History), no. M.21460. Most of the new material described here belongs to an excellently preserved herd excavated from site SHK II in 1935. According to Dr. L. S. B. Leakey the herd was discovered in clays about 300 feet from a living floor near the base of the upper part of Bed II. It is likely that the herd was entombed in a muddy swamp (into which it had perhaps been driven by the men inhabiting the living floor?). The minimum number of individuals in the herd, based on the metatarsals, is nine or ten, all but two of which are juvenile or young animals.

MATERIAL. The list of skull parts comprises the following:

M.21462	adult frontlet (Pl. 5)
M.21464	cranium and upper teeth of a young adult (Pls. 5, 7C)
M.22436	two mandibles with complete adult dentition (probably the same individual) (Pl. 8A)
M.22378	adult mandible
M.22371	adult basioccipital (Pl. 7B)
M.22372–77 M.22380–83	maxillary and mandibular pieces, mostly sub-adult

The following pieces from the 1960 dig are also assigned to *P. recki*:

1960, FLKN I, layer 1–2–3, 627 . .	maxilla and upper teeth
,, ,, trial trench, 6176 . .	fragment of juvenile maxilla
,, ,, layer 1, 1281, 1327, 1511 .	fragments of juvenile maxillae
,, ,, layer 3, 6044 . . .	fragment of right mandible
,, FLK I, B.119	fragment of right mandible
,, FLKN I, layer 5	right horn core (Pl. 7A)

The following three horn cores, from years other than 1935 or 1960 are also included:

1955, BK II, 71

B.M. (N.H.), M.14513, Bed I, probably a surface find (Pl. 7A)

B.M. (N.H.), M.15862, Kanjera, Kenya. (Previously identified as this species by Dr. A. T. Hopwood.)

The frontlet M.21462 (Pl. 5) has horn cores which are oval in cross section without any flattening of the lateral side or tendency to form a postero-lateral edge. Horizontal ridges can be seen on the lower antero-lateral parts of the horn cores. They are not very steeply inserted on the frontals, their basal portions rise parallel to one another then bend backwards and outwards, and taper gradually to a point. The supraorbital pits are small and the level of the frontals between the bases of the horn cores is higher than the orbital rims. The left orbital rim is complete in its dorsal part and is rather wide compared with the width apart of the pedicels of the horn cores.

The horn cores on the cranium M.21464 (Pl. 5) are shorter and their distal parts are not so strongly bent backwards as in M.21462. From the appearance of the surface of the horn cores it can be inferred that M.21464 is a younger individual than

M.21462, but while further growth could have caused the distal parts to bend back as strongly as in M.21462, their tapering towards the tip would not have been drawn out over such a long distance. The *Phenacotragus* horn cores can be distinguished from those of *Gazella wellsi* by being more nearly parallel at the base in anterior view and then more outwardly divergent in their distal parts. They are also more symmetrical in cross section and lack the flattened lateral surface of *G. wellsi*.

The orbital rims are again wide in M.21464, and the braincase is very narrow. The braincase looks as if it is shorter than in a gazelle and its top surface is less flat in profile than in males of *G. thomsoni* or even *G. rufifrons*. Preorbital fossae are present and are about as extensive and deep as in a female *G. thomsoni*. The basioccipital is like that of a young *G. thomsoni* or a *G. dorcas*; no very profound conclusions can be drawn from this since the basioccipitals of all young gazelles look similar to *G. dorcas* and it is not surprising that one in a related genus does also.

A separate basioccipital, M.22371 (Pl. 7B) is from an adult skull, possibly M.21462, and this is quite unlike most living gazelline forms. The anterior tuberosities are close together and the longitudinal ridges are almost non-existent. The nearest approach to this sort of basioccipital is found in some individuals of *G. bennetti* of India, and an almost identical one is seen in the type cast skull of *P. recki* in the British Museum (Natural History). An isolated nasal bone has survived; it is not complete anteriorly, but even in this state it is longer than in any living gazelle.

At a fairly late stage of the work it was noticed that if only an isolated horn core of M.21464 had survived instead of the whole cranium it would have been very much like the four horn cores at the end of the list—1960 FLKN I (?),[8] 1955 BK II 71, M.14513 and M.15862. The last one, from Kanjera, had in fact already been labelled as *Phenacotragus recki* by Dr. A. T. Hopwood (see Kent 1942). But if these four horn cores are of the same species as M.21464, and if M.21464 and M.21462 were of the same species as the cast of the type skull—M.21460—the problem arises of allocating the horns and skulls to the different sexes. The four horn cores at the end of the list are so much smaller than M.21460 that they must be the females and M.21460 the male. None of the last four shows any signs of being from young animals, nor is it conceivable that they could grow into the shape of M.21460. These presumed female horns differ from the male by being less backwardly bent, probably less outwardly divergent in their distal portions and, in M.14513, in tapering to a point over a much shorter distance. As in the Olduvai *Gazella wellsi* they are more bulky than in the females of living gazelles. Females of other gazelline genera except *Antidorcas* are hornless.

While M.21464 may be accepted as a female on the assumption that its horn cores have almost stopped growing, it is difficult to place M.21462. It is an adult animal, and if a female its horns are unexpectedly large. On the other hand they are smaller than in M.21460. It would be a great help if the horizon of M.21460 were known, for over such a long period of time as is represented at Olduvai changes in body size of the species or immigrations of different *Phenacotragus* species are quite possible. The probability is that M.21462 is male.

[8] The number has become illegible, but the horn core is from layer 5.

It is interesting to note in the supposed female horn cores of *P. recki*, that while the basal parts are bulky for their size, the distal parts are either short as in M.14513, or if they are long then the whole length of the distal parts has a much reduced girth compared with the basal parts as in the horn core from 1960 FLKN I, layer 5 (and to some extent in M.21462). Such a pronounced reduction in girth of the distal parts is not known in the horns of female living gazelles. In these, the female horn cores are uniformly thinner than those of males down their entire length ; as may also be seen in the two horn cores assigned to the *Gazella* species of group (B) at Olduvai (Pl. 7A).

Upper teeth

The upper teeth of *P. recki* are undoubtedly gazelline but the molars differ from living gazelles and from the Bed I teeth supposedly belonging to *G. wellsi* in the more prominent mesostyle on the outer wall and in the tendency towards a concave outer wall of the posterior part of the tooth. In M.21464 (Pl. 7C) the junction of anterior and posterior parts of the molars is wider than in gazelles at the same stage of wear owing to the less deep incision of the inside wall. The M^3s of M.21464 have not completely erupted, and they show the hypsodonty of *P. recki*. The length from the neck to the occlusional surface down the outside edge between the anterior and posterior lobes is 3·00 cm., while the length of the base of the erupted part along the jaw line is 1·32 cm. The length of the adult premolar row can be measured on FLKN I 627, and on the type skull, and can be approximately estimated for M.21464 in which P^2 is missing. It is clear from Text-fig. 6 and from previously given values that the premolar row is probably shorter than in living gazelles and may be as short as in *G. wellsi*.

Some teeth from the 1960 dig in FLKN I, upper molars 121 and 122, two unnumbered upper molars and a piece with $P^3 + P^4$, are larger than the other teeth from that site and have the morphology of a *Phenacotragus*. On Text-fig. 5 the length of 122 has been plotted on the assumption that it is an M^2, and it falls well within the possible size range of the Bed II species. However it is true that 122 is only very slightly smaller than the M^2 of the upper dentition FLKN I, 1662, already mentioned in the account of *G. wellsi*, and the size of 1662 is matched by fragments of lower jaws from Laetolil (1959, nos. 150, 151, 294 and 443 + 444—see Appendix II) which look as if they belong to a larger species of *Phenacotragus* than is represented by the SHK II herd. The previously mentioned large gazelline limb bones from Bed I (scapula FLKN I, 1467, femur FLKN I, 1027 and others) could go with these teeth remains. So there is evidence of at least one larger sized gazelline species in Bed I and at Laetolil, but it cannot be definitely regarded as closer to *Phenacotragus* than to *Gazella wellsi*.

Mandibles

The lower molars are distinguishable from gazelles by having medial walls of the anterior and posterior lobes which are less curved outwards from the body of the tooth in question, and by having still less of a tendency towards the development of

goat folds. In addition the posterior deepening of the horizontal ramus (Pl. 8A), involving a change in direction of its lower edge at about the level of M_2, is more pronounced than in gazelles, and the ascending ramus of the left side of M.22436 is less tall than in gazelles. The tooth differences alone are not so surely perceptible in older individuals, and unless the mandible itself is also well preserved the generic separation may not be certain.

While the separation of the mandibles from those of *G. wellsi* in Bed I may seem well established at first sight, it must be noted that only the left M.22436 among the *P. recki* mandibles is both adult and complete, and that only FLK I, G.323 from *G. wellsi* is really adequate for comparison with any other species. Also the juvenile bones of both species are similar—M.22372 of *P. recki* has an ascending ramus shaped more like that of *G. wellsi* than have adults of its own species, and a number of juvenile mandibles in Bed I (FLKN I, layer 1–2–3, 231; layer 1, 1310; layer 5, no number; FLK I, 8 and 188) are like *Phenacotragus* in their tooth morphology and in the shape of the horizontal ramus anteriorly. But if the juvenile mandibles from Bed I are referred to *P. recki* then the older mandibles alone are left as *G. wellsi* which is clearly an unsatisfactory situation. None the less, by observing the characters of shape and height of the ascending ramus, depth of horizontal ramus and course of its lower edge, and the morphology of little-worn adult molars, a distinction should be possible with adequate samples.

Concerning the premolars, the posterior part of the inner wall of P_4 is closed in M.22436 and P_2 is very much reduced, but in M.22378 the posterior part of the inner wall of P_4 is open and the socket of P_2 suggests that it was larger than in M.22436.

The principal reasons for assigning this herd of gazelline antelopes to *Phenacotragus recki* lie in the resemblance of the horn cores and frontals region of M.21462 and M.21464 to the cast of the type skull (Pl. 6), the resemblance of the upper teeth morphology and proportions, the similarity of the basioccipitals and the long nasal bone found with the 1935 herd.

The differences of the type cast from the frontlet and cranium M.21462 and M.21464 are only minor. The type skull is larger, and its longest molar, M^2, is only barely shorter than the upper molar FLKN I, 122 which was considered perhaps too large to belong to the same species as the SHK II herd. Also the basal part of the type skull's only surviving horn core is longer before bending backwards and a little more divergent in anterior view. The course of its upper parts is rather more of a spiralization than a simple backwards and outwards bend. No transverse ridges occur towards the base. The basioccipital is longer with a deeper valley between the anterior tuberosities, the descending flanges of the basisphenoid originate more anteriorly, the upper molars have more sharply pointed inner lobes and lack marked concavities of the posterior halves of their lateral walls, and the preorbital fossa is a little smaller. The first four differences (size, longer basal part of the horn core, more divergent, spiralization) could be due merely to age or sex factors, while the presence or absence of transverse ridges on horn cores is a variable character within other gazelline species. The last five differences are insufficient to place the 1935 herd beyond a legitimate range of variation from the already named type skull,

especially when the unknown horizon of the type is remembered. However, since the horizon of the type is unknown, since the above differences might not be due to age or sex, and since there is evidence of a larger gazelline species which might well be conspecific with the name-bearing type of *Phenacotragus recki*, then it is still possible that further finds will show that the 1935 herd should be placed in another and smaller sized species of *Phenacotragus*. At present one could not write two clearly distinct diagnoses with any firm basis, and the fossils may be from one lineage which varied in size at different periods.

The limb bones of PHENACOTRAGUS RECKI *(Pl.* 8B, C)

Schwarz (1937) thought that within the Antilopini, *Phenacotragus* was related to *Aepyceros*, the impala. This question will be discussed later, and in the following account of limb bones *P. recki* will be compared both with the impala and with living gazelles.

Pelvic girdle

Among the bones of the herd excavated from SHK II in 1935 are two sides of a sub-adult pelvic girdle (M.22451), two juvenile left sides (both numbered M.22391) and a juvenile right side (M.22392). The minimum number of individuals represented is three. The sub-adult girdle is smaller than in *G. thomsoni*. It differs from living gazelles only in that the articular facets at the back of the acetabulum are not so close to one another, but this difference might disappear in older individuals.

P. recki is unlike the impala in not having a low rear part of the pubic symphysis, in its well marked medial origin for the rectus femoris muscle, and probably also in the origin for the iliacus extending backwards along the lowest part of the lateral side of the ilium. The outline of the top part of the front edge of the ilium cannot be seen in *P. recki*.

Femur

There are two sub-adult femora in which the epiphyses have started to close (M.22452–53), four juvenile femora (three numbered M.22422 and one M.25038), and a juvenile distal and proximal end (M.22423 and M.22393). The minimum number of individuals in the herd based on femora is four.

The two sub-adult bones, almost certainly from the same individual, differ from living gazelles in the following respects : the stem supporting the articular head is more massive in medial view of the proximal end. The effect of this, in conjunction with the deeper rear edge of the acetabulum of the pelvis, would be to restrict the backwards stride of the femur compared with modern gazelles. But this character may not have persisted in older animals ; in *G. thomsoni* it is more marked in young animals. Secondly the medial end of the proximal articular head lies relatively more posteriorly in the fossil. This may best be seen by laying the bone on a horizontal surface with the anterior side upwards. The articular head of the fossil is then in more or less a horizontal plane while that of a living species is directed more diagonally. The effect of this would be that the distal end of the

femur in a living species swings further outwards as it is protracted than in *P. recki*. Thirdly at the distal end of the femur, the side of the lateral condyle looks more convex behind the pit for the femoro-tibial ligament ; this is best seen in ventral view. Lastly, the hollow for the ligamentum teres on the articular head is deeper.

P. recki is unlike the impala in the position of the gluteus accessorius insertion and the absence of a separate crest above the accessorius for the rear parts of the vastus lateralis. The convexity of the distal lateral condyle and the deep hollow on the articular head are, however, nearer to the condition of the impala than gazelles are. Older individuals of *Phenacotragus* would be needed to see which genus it resembled in the outline of the top of the great trochanter.

Tibia

There are two sub-adult tibiae in which the sutures are closing (M.22454–55) ; they are almost certainly from the same individual and moreover from the same animal which supplied the sub-adult femora (M.22452–53). In addition there is an adult distal end of a shaft (M.22394) and eight juvenile tibiae (M.22395, M.22424, three of M.22425, two of M.22426 and M.22427). The minimum number of individuals is seven.

They are hardly distinguishable from gazelles except in the following respects. The long axis is curved forwards at the top and bottom to an extent which is intermediate between living gazelles and the 1960 fossil tibiae from FLK and FLKN. Distally the medial malleolus is neither so curved nor so long as in living gazelles. Despite being rather smaller than *G. thomsoni*, the sub-adult tibia falls above the average values of *G. granti* and *G. thomsoni* for thickness and almost on the mean value of *G. granti* for length compared with that of the femur (Text-figs. 9, 10).

The *Phenacotragus* tibiae differ from the 1960 fossils in having a less convex posterior surface towards the top and in the longitudinal digital flexor ridge being closer to the lateral side. The cnemial crest is less concave on its lateral surface and the whole axis slightly less turned forwards at top and bottom, but these last two differences might disappear in more elderly animals. The ridge for the longitudinal digital flexor actually lies slightly further from the lateral edge of the bone than in *G. thomsoni* but perhaps not so far as in *G. granti*.

Phenacotragus is gazelline and not like the impala in having a tubercle on the top articular surface anterior to the attachments for the cruciate ligaments and ligaments from the menisci, and in having the longitudinal digital flexor ridge further from the medial edge of the posterior surface (but note the 1960 fossils on page 70). The shorter medial malleolus, although unlike living gazelles, is not likely to show relationship to the impala, and the other details of the distal end are as in living gazelles.

Metatarsal

There are two adult metatarsals (M.22464–65) which are from different individuals, one of them probably the same as that with the pelvic girdle M.22451, femora M.22452–53 and tibiae M.22454–55. There are also twelve juvenile specimens (six

of M.22428, three of M.22429, M.25035 and M.25037). The minimum number of individuals is nine or ten, which is also the minimum number for the herd.

They are not distinguishable from the Olduvai 1960 metatarsals, and are only doubtfully distinguishable from living gazelles by a proportionately larger naviculo-cuboid facet. Text-fig. 11 shows that the two adult bones fall beyond the range of living gazelles, but those of the younger individuals do not. The adult ones are relatively thicker than in living gazelles, as can be seen on Text-fig. 10, but not so thick as the 1960 metatarsals. They differ from *G. thomsoni*, but not so clearly from other gazelles, by having the top articular surface less upcurved at the front, and by having a lower back part of the top articular surface.

In the impala there is a slightly better marked longitudinal groove on the anterior surface, the ectocuneiform facet is not so upcurved in medial view, there is a short ridge bounding the medial side of the lateral extensor tendon at the top of the anterior surface and the anterior flanges just above the distal condyles are poorly developed.

Astragalus

There are eleven astragali (nine of M.22398, M.22457 and M.22461). It is more difficult to pair off right and left ones than it is with the long limb bones but the minimum number of individuals appears to be six. The range of variation is so great that reliable differences from gazelles are few. The excavation of the lower part of the lateral side is perhaps deeper than in living gazelles but not so deep as in the 1960 fossils from FLK and FLKN. They differ from both living gazelles and the 1960 fossils by having a narrower and sharper anterior rim on the top half of the lateral side.

Phenacotragus recki is undoubtedly gazelline and unlike the impala in the depth of the hollow on the lower lateral side, and in the lack of a deep indent on the lower posterior side.

The astragalus 1960 FLKN I, layer 3, 6253 may belong to *P. recki*.

Naviculo-cuboid

There are twelve naviculo-cuboids (six of M.22434, four of M.22435, M.22458 and M.22462). The minimum number of individuals is seven. They cannot be distinguished from living gazelles, but the posterior wall projects further backwards than in the 1960 fossils. They differ from the impala in that the outline of this posterior projection is not concave along its upper edge, in the lack of a hollow on the lower back part of the medial wall and in the lack of a facet to fit into the hollow on the posterior side of the astragalus. Since *P. recki* does not have the hollow on the astragalus the corresponding facet of the naviculo-cuboid is necessarily absent.

Scapula

The remains of six scapulae are found with the herd from SHK II; they are numbered M.22385, two of M.22386, M.22387, M.22442 and M.22443. The minimum number of individuals based on scapulae is four.

They cannot be satisfactorily distinguished from the 1960 fossils or from living gazelles, but it may be true that the medial side of the tuber scapulae is more concave (unless this is characteristic only of young animals).

Humerus

There is a pair of fully adult humeri (M.22404 and M.22406), a sub-adult one on which the epiphyses are closing (M.22444), four juvenile bones (three of M.22405 and M.22407), together with a distal end (M.22407). The minimum number of individuals is five and M.22444 probably came from the same individual as the pelvic girdle M.22451, the femora M.22452–53 and the tibiae M.22454–55.

They are not different from the 1960 fossils. The proximal end differs from living gazelles in having a protuberance on the floor of the bicipital groove in anterior view. The relative thickness of both the adult and the sub-adult humeri is greater than the mean value in *G. granti*, but only the adult one exceeds the mean for *G. thomsoni*.

The fossil agrees with gazelles and is unlike the impala in that the top of the greater tuberosity does not approach so closely to a horizontal position in anterior view, in the absence of a bony projection behind the infraspinatus insertion, in the absence of a ridge on the lateral side for the extensor carpi radialis origin and in the absence of a vertical ridge in the coronoid fossa above the distal condyles. The distal lateral groove may be less wide than in gazelles, but is a doubtful character difference.

Radius and ulna

There are nine radii from the SHK II herd. M.22410 and its olecranon M.22411 are fully adult and belong with the humeri M.22404 and M.22406. M.22445 and its olecranon M.22446 are sub-adult and go with the humerus M.22444. The other specimens (two of M.22388, M.22389, two of M.22408, two of M.22409 and two olecranons numbered M.22411) are all fragmentary or young ones. The minimum number of individuals is six. Text-fig. 12 includes a drawing of the proximal articular surface of M.22410.

In comparison with *G. thomsoni* the antero-medial edge of the medial facet at the proximal end is more evenly rounded; in comparison with *G. thomsoni* and other gazelles the lateral facet at the proximal end is more flattened, the top of the shaft shows a little less torsion on the lower part, the ridge forming the medial boundary of the scaphoid facet extends further ventrally and the extent of the cuneiform's articulation on the radius is greater. The lateral tubercle on the older radius is large and situated high as in living gazelles, on the younger sub-adult one it is smaller and low as in the impala. In the ratios of least thickness/length and length/length of humerus both the adult and sub-adult radii are less cursorially advanced than the means for *G. granti* and *G. thomsoni*. Three proximal ends from the 1960 dig, FLKN I 1217, unnumbered and 6106, can be assigned to *P. recki*.

The radius of *P. recki* is distinguished from the majority of the 1960 radii described above by the rounded edge of the medial facet at the top, the cuneiform's articula-

tion on the radius being greater, and possibly by the medial facet at the top being more indented posteriorly.

The impala agrees with *P. recki* in the flattened surface of the lateral facet, in having less torsion of the stem, the medial boundary of the scaphoid facet extending far ventrally, and the cuneiform's articulation on the radius being wide. But in other characters the impala is different from *Phenacotragus* ; it has a hollow below the medial side of the medial facet, two forward projections of the medial facet, and distally that part of the scaphoid facet on the posterior surface is longer.

Metacarpal

There are four adult metacarpals—M.22412, M.22449–50 and M.25036. The middle two of them could be from the same sub-adult individual mentioned before, while the last is provisionally placed with the humeri M.22404 and 22406 and the radius M.22410. There are also five fragmentary or young metacarpals (M.22390, M.22413, two of M.22414 and M.22430). The minimum number of individuals represented is five. The proximal articular surface of M.25036 is illustrated in Text-fig. 12. The metacarpals from the three adult or sub-adult individuals are

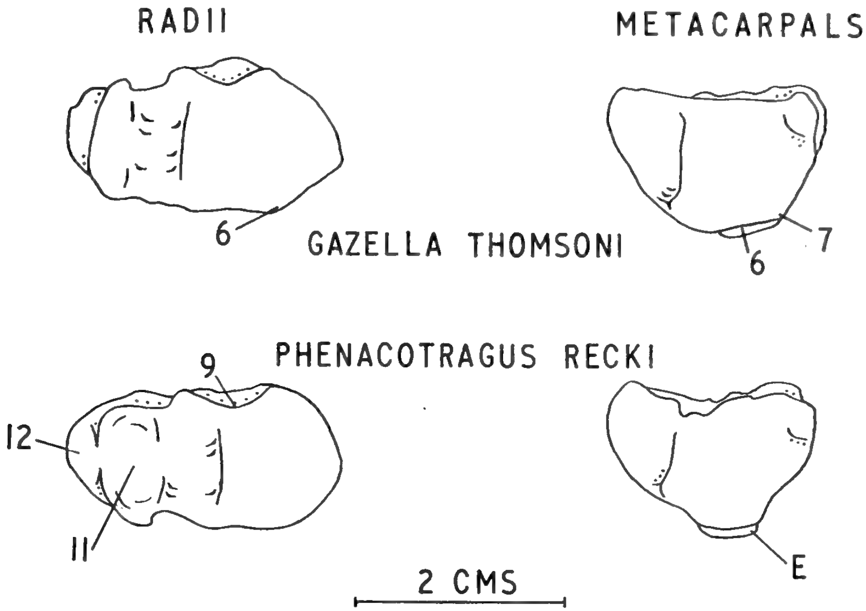


FIG. 12. Proximal articular surfaces of radii and metacarpals of *G. thomsoni* and *Phenacotragus*. The lateral side is on the left and the posterior side towards the top. On the metacarpals 7 shows the angled corner of the magnum-trapezoid facet and 6 the front edge of the facet with E, the extensor carpi radialis insertion, in front of it. On the radii 6 shows the antero-medial angle of the medial facet, 9 the posterior indentation of the medial facet, 11 the lateral facet, and 12 the lateral tubercle.

relatively thicker than in the measured living gazelles, and the fossils' mean for the ratio length of metacarpal/length of humerus is the same as that of the much larger *G. granti*.

They differ from living gazelles and from the 1960 fossils in having the extensor carpi radialis insertion more transversely compressed so that it is more localized and projects further anteriorly. The antero-medial side of the magnum-trapezoid facet is not so prominently angled as in *G. granti*, and the back edge of the top articular surface as a whole is more concave in M.25036. This last character is not the same as the more localized indentation mentioned as metacarpal character (2) in Gentry (in preparation). The proximal end FLKN I, 5149 from the 1960 dig and an unnumbered bone from FLKN I, trial trench, layer 3, may belong to *Phenacotragus recki*. The anterior proximal foramen is better developed than in living gazelles even in the adult fossil bones. Only one out of the four adult or nearly adult bones has an indented posterior edge of the top articular surface.

The impala differs from *P. recki* and living gazelles by having no anterior proximal foramen, a more deeply hollowed posterior side of the shaft, and the lateral end of the posterior edge of the magnum-trapezoid facet forming abackwardly pointed projection.

Phalanges

There are a large number of phalanges of *Phenacotragus recki* (M.22466–78). The first phalanges are like living gazelles, rather than the impala, in having two concave areas, one above the other, at the top of the posterior surface. However the flanges bounding the more distal of the concavities are less well developed than in gazelles, and this brings the appearance of the fossils somewhat closer to the impala.

Comparison of the limb bones of living gazelles, PHENACOTRAGUS RECKI *and those from the* 1960 *dig in Bed I*

Although the bones of *Phenacotragus* are more massively proportioned than those of living species, they are less massive than those of the 1960 dig in Bed I. This may be due to continuing skeletal evolution in the African Antilopini through the period represented by the basal part of Bed II; but part of the cause may be that the ontogenetic age of the two *Phenacotragus* individuals is less than the 1960 fossils or that the *Phenacotragus* may be females and the 1960 ones males.

The characters in which the fossils differ from living gazelles can be divided into three groups:

A. Those in which the 1960 fossils and *Phenacotragus* agree.
B. Those in which the Bed II *Phenacotragus* is intermediate between the 1960 fossils and living gazelles.
C. Those in which the 1960 fossils or *Phenacotragus* are distinctive.

A. The characters in this group possessed by the fossils are:

(1) the shorter medial malleolus of the tibia;
(2) the flattened lateral facet of the radius;

(3) the ventral extension of the medial side of the scaphoid facet at the distal end of the radius ;
(4) perhaps a lesser torsion of the radius stem ;
(5) the better developed anterior proximal foramen of the metacarpal.

B. Character differences from living gazelles in which the Bed II *Phenacotragus* is intermediate between the 1960 fossils and Recent species. The characters in this group are :

(6) the degree of convexity of the distal lateral end of the femur ;
(7) the course of the long digital flexor's ridge on the posterior surface of the tibia ;
(8) the curving forwards of the long axis of the tibia at its top and bottom ends ;
(9) the size of the naviculo-cuboid facet at the top of the metatarsal ;
(10) the depth of excavation of the lower lateral side of the astragalus ;
(11) the size and position of the lateral tubercle at the top of the radius ;
(12) the indentation, or lack of it, on the posterior top edge of the metacarpal.

Many of these characters in the fossils are similar to *Aepyceros*, namely (1), (2), (3), (4), (6), (7), (9) and (11). In addition the deep hollow on the articular head of the femur of *Phenacotragus* and the shape of the posterior edge of the lower lateral side of the astragalus are not unlike *Aepyceros*. This might suggest that a relationship to that genus should be considered. However characters (1), (3), (6), (9), (10), (11) and perhaps (2) and (7) of the fossils are also like *Redunca* and *Kobus*, and characters (1), (4), (6), (7), (9) and (12) are like the Alcelaphini. Moreover characters (1), (4) and (9) at least may reasonably be taken to be more primitive in the fossils than in living gazelles. So the real situation is that the Olduvai fossils have a greater number of characters in common with other antelopes than have living gazelles.

However this is not the end of the story because a check at the British Museum (Natural History) on the limited number of limb bones assigned to the Pontian gazelles of Pikermi showed that they were like the Olduvai fossils only in characters (9) and perhaps (11). Two Pontian metacarpals were available for checking character (12) ; in one the posterior edge was indented and in the other it was not. In characters (2) and (3) the Pikermi radius is like those of living species, in (5) the two metacarpals are like *Aepyceros*, and in two astragali the excavation of the lower lateral side is less deep than in the Olduvai fossils but wider than in living gazelles (10). The state of the Pontian fossils was not satisfactorily ascertainable for characters (1), (4), (6), (7) and (8).

So while the conclusion from the African evidence alone could well be that the limb bones of the gazelline species at Olduvai were evolving towards the condition of living gazelles and away from a condition similar to the impala and to other tribes of antelopes, what there is of evidence from Pikermi does not fully support this conclusion. The fact that the lateral facet of the Pikermi gazelle's radius is not flat (2), that the medial side of the scaphoid facet is not extended ventrally (3), that the metacarpals lack an anterior proximal foramen (if this be not an age effect) (5), and that the excavation of the lower lateral side of the astragalus is no deeper

than in living gazelles (10), might all be evidence that the Pikermi species were not close to the ancestry of African living or fossil gazelline species. Or it might be true that they were close to the ancestry of living gazelles but not to that of East African gazelline fossils.

C. Characters possessed only by the 1960 fossils or by *Phenacotragus*. One or two characters of the 1960 fossils are distinctive, namely the less flattened posterior surface of the tibia, the lack of projection of the posterior wall of the naviculo-cuboid in medial view, and the possibly better developed unciform projection on the top articular surface of the metacarpal. The Bed II *Phenacotragus* is distinctive in the thinner anterior rim on the top of the lateral side of the astragalus (unless this is due to youthfulness), the wider cuneiform articulation on the radius and a transverse compression on the extensor carpi radialis insertion at the top of the metacarpal.

The Olduvai fossils are like the springbok only in the flatness of the lateral facet of the radius, the size and position of the lateral tubercle, perhaps in the length of the scaphoid projection distally, and in the short medial malleolus of the tibia. In addition the vertical ridge at the top of the femur 1960, FLKN I, 1027 is like the springbok. It cannot be said on the basis of these characters nor on the basis of those characters of the metacarpal and radius tops in which living gazelles are not uniform (antero-medial corner of magnum-trapezoid facet of the metacarpal, shape of antero-medial edge of the medial facet of the radius, shape of the side of the medial facet and indentation of the posterior side of the medial facet), that either the Bed I or Bed II fossils resemble *Antidorcas* more than *Gazella*.

VI. RELATIONSHIPS OF *PHENACOTRAGUS RECKI* (SCHWARZ) AND *GAZELLA WELLSI* COOKE

It was Schwarz's view (1937) that the Alcelaphini (hartebeests and wildebeests) should be included in the subfamily Antilopinae. According to him *Phenacotragus* could be placed between *Aepyceros*, the impala, and *Beatragus*[9] as one of a trio of intermediate genera passing from gazelles to hartebeests and showing the reality of the relation between them.

The position maintained here involves changes of emphasis in Schwarz's views rather than their outright rejection. From its skull characters *Phenacotragus* is taken to be definitely gazelline and to have a close phyletic relationship or perhaps even a generic identity with *Antidorcas* of South Africa. *Aepyceros* is regarded as a somewhat isolated genus, certainly not like *Phenacotragus*, certainly not gazelline, and probably closer to the Alcelaphini than to any other group. Schwarz thus rightly pointed to the resemblances of *Aepyceros* and *Beatragus* as showing a relationship between them, but any resemblances found between *Aepyceros* and *Phenacotragus* would be, in my view, the result of chance, parallel evolution or of unchanged inheritance from a common ancestral condition. However it is possible that at a more remote level the Alcelaphini, or at least the hartebeests among them,

[9] The Hunter's antelope or Tana River hartebeest—*Beatragus hunteri*—is the only species in this genus, which has occasionally been included in *Damaliscus*.

are related to the gazelline/caprine stock, and this involves a reapproach towards Schwarz's views. Indeed it is further possible that *Phenacotragus* and *Antidorcas* could be closer to the hartebeest ancestry than *Gazella* itself, particularly since *Phenacotragus*, *Antidorcas* and the hartebeests[10] are all limited to Africa whereas *Gazella* occurs also in Eurasia. But this is speculative as yet and it is only necessary here to show that phenetically *Phenacotragus* is gazelline and close to *Antidorcas*, that *Aepyceros* is very ungazelline, and that therefore the two are unlikely to be closely related.

Characters in which PHENACOTRAGUS *differs from* AEPYCEROS

The following differences in the skulls and teeth between *Aepyceros* and *Phenacotragus* can also be taken as separating *Aepyceros* from other gazelline genera.

1. The horn cores of the impala are unlike those of *Phenacotragus* in their wide divergence from the pedicel, in their long even curvature outwards and backwards, and in the abrupt turning inwards and forwards of the terminal portions. *Beatragus* has very similar horns, and those of *Alcelaphus* can be seen as a short, thickened version of the same basic shape.

2. The horn cores arise further behind the orbits in the impala than in *Phenacotragus*.

3. The supraorbital foramina are much wider apart in the impala than in *Phenacotragus*. This is an easily measurable character, and Text-fig. 13 shows the distance between the foramina expressed as a percentage of the orbital width in some selected

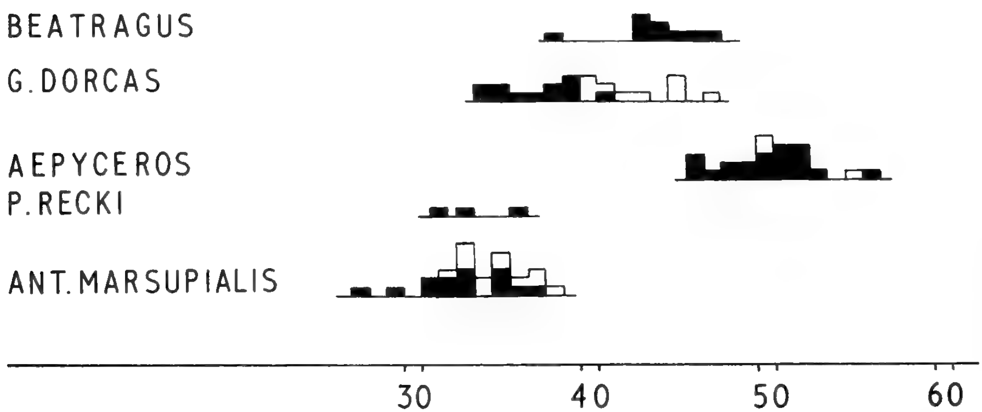


FIG. 13. Histogram of width of supraorbital foramina/orbital width. ×100. Unblackened readings indicate females and blackened ones males, but the sexes of *Beatragus hunteri* and the *Phenacotragus* were not determined. *Phenacotragus* is clearly most like *Antidorcas marsupialis* in this ratio. Ten of each sex of *G. dorcas* were measured, and the females had the supraorbital foramina wider apart than in the males.

[10] One hartebeest is known from the Lower Pleistocene of India (Pilgrim 1939 : 67), doubtless a wanderer from Africa.

antelope genera. In *Phenacotragus* and the springbok the foramina are very close together and there is no overlap with the impala. The readings for *Gazella dorcas*, as a representative gazelle, and for *Beatragus* are intermediate. The supraorbital foramina are situated further forwards from the base of the horn pedicels in the impala, and this also helps to give this region of the skull a quite different appearance from any gazelline species.

4. The braincase of *Phenacotragus* (M.21460) looks a little shorter than in the living *Gazella rufifrons*, which means that it is certainly shorter than in most other gazelles, but the braincase of the impala is still shorter than in *Phenacotragus* or any gazelline species.

The facial region of the impala is lengthened and the back edge of the tooth row in adults lies further forwards relative to the orbits than in the type skull of *Phenacotragus*. There is a size allometry for this character in gazelles with bigger species having the tooth row further forwards, but the tooth row of the impala is still further forwards than in the largest gazelles. The long face of the impala cannot safely be regarded as a separate character from its short braincase, because both may be only consequences of more posteriorly situated orbits. It is likely that mechanical factors and questions of support are involved here, since there does seem to be a relation between the two dimensions among the Alcelaphini, Antilopini and Caprinae, with *G. thomsoni* and *Alcelaphus* species at opposite extremes among living forms.

5. The anterior tuberosities on the basioccipital of the impala are close together as in *Phenacotragus*, but their shape is different and there are strongly marked longitudinal ridges behind them.

6. The walls of the central cavities on the occlusal surfaces of the upper molars have anterior and posterior localized infoldings in the impala but not in *Phenacotragus*. The impala also shows a greater curvature of each central cavity in the unworn state (see Text-fig. 14). These are not characters which would allow certain identification of isolated teeth, but they are consistent and recognizable in series of teeth. Among gazelline genera only *Antilope* has much tendency towards similar infoldings but the shape of its central cavities as a whole is different from either *Aepyceros* or other gazelline genera.

7. The medial walls of the anterior and posterior lobes of the lower molar teeth are more convex in the impala, and the lateral walls of the lobes too are more evenly rounded and less acutely pointed than in living gazelles or *Phenacotragus*. The central cavities on the lower molars are distinctively shaped with more transverse constriction of their mid-points than at either end (see Text-fig. 15). The lower teeth of *Antilope* and the lower teeth in the British Museum (Natural History) supposedly of *Helicotragus* and *Gazella mytilinii*, are similar to *Aepyceros*. The lower molars of *Phenacotragus* are at the opposite extreme with their fairly straight medial walls. The functional meaning of the diverse patterns of lower molars in antelopes is not understood, nor to what extent there is a necessary correlation between the complicated folding of the walls of the central cavities of the upper molars and the varying characters of the lower molars. The combination of upper and lower molars similar

to *Aepyceros* in *Antilope* suggests some correlation. In any event, the pattern of dental evolution is very different in *Phenacotragus* and *Aepyceros*.

8. The medial wall of P_4 in the impala has the anterior valley closed off, i.e. the valley has become an internal cavity and the wall bounding it is complete. This is unlike any gazelline species except the Asiatic *G. gutturosa*, *G. picticaudata* and *G. sinensis*, but it is found in all living Caprine and Alcelaphine genera.

9. The ramus of the lower jaw of the impala is rather shallower than in *Phenacotragus* or other gazelline species and the ascending ramus slopes more.

In all the characters listed above the impala is not only unlike *Phenacotragus* but shows slight resemblances to the Alcelaphini—more than does any gazelline genus. Also unlike Antilopini but like the Alcelaphini is the fact that the median indentation at the back of the palate in the impala projects further anteriorly than the lateral indentations. The impala obviously lacks the extreme skull specializations of *Alcelaphus* and *Damaliscus*, and except for the similarity of its horns to those of *Beatragus* there is no reason to suppose it is particularly closely related to them. Fossil finds of the Alcelaphine faunas of earlier periods in Africa may help to close the gap. Other differences between impala and *Phenacotragus* skulls are indecisive in assessing relationship, e.g. the larger auditory bulla of the impala, its loss of a preorbital fossa and its reduced ethmoidal fissure. The size of the bulla can differ even in closely related antelopes, and the last two characters are known to show parallel changes in different lineages. The presence of a long foramen between the premaxilla and maxilla in the impala and the strong lateral flanges on the front of its nasals are probably a peculiarity of the species, different from either Antilopini or Alcelaphini.

Only three firm similarities can be found in the skulls of *Phenacotragus* and the impala. These are :

1. the high level of the frontals between the horn pedicels compared with the level of the orbital rims ;

2. the long nasals ;

3. reduction in the size of P_2.

All three characters are also shared in common between *Phenacotragus* and the springbok. In the high level of its frontals *Phenacotragus* looks much more like the springbok and not at all like the impala ; the many other differences in this region of the skull quite overshadow the effect of this one resemblance to the impala. The nasals of *Phenacotragus* are so narrow as to remind one of a hartebeest or a reduncine, and are not very like those of the impala in anything other than being narrower than in gazelles ; nor in fact are they very much like the springbok.

In writing that *Aepyceros*, *Phenacotragus* and *Beatragus* were genera which seemed to show the connection between the gazelle and hartebeest groups, Schwarz was not very precise, but if his view were true, presumably one ought to be able to see a number of characters in common, or even gradations of characters, between the hartebeest and the gazelle extremes. In fact this expectation has not been fulfilled. While the impala shows tendencies towards the characters of the Alcelaphini,

Phenacotragus shows no positive likeness whatever to the impala. There is a sharp break along this line from gazelles to hartebeests, whatever may be the case with undiscovered fossils.

It is because of the slight but definite alcelaphine tendencies in the skull of the impala and the total absence of convincing resemblances to gazelles that it cannot be thought of as simply a rather aberrant or even the most aberrant known gazelline genus. In addition its limb bones have an unusually high number of distinctive characters, very few of which are shared by *Phenacotragus*, and show a high total of character differences from gazelles. It is evident that the skeletal adaptations for pronking (a jumping gait) in the springbok (and those for stotting in gazelles?) are quite different from those for leaping high in the impala. As in its teeth, so too in its limb bones, morphological adaptation has evolved along different lines. One can only regard the impala as the successful occupant of an ecological niche rather remote from any others, and I think it may best be classified by being included in the tribe Alcelaphini. A fossil horn core 1957, BK II, 662 shows the presence of *Aepyceros* in the upper Bed II fauna of Olduvai, and Arambourg (1947) records it from Omo.

Characters in which PHENACOTRAGUS *agrees with* ANTIDORCUS MARSUPIALIS

After rejection of the postulated relationship of *Phenacotragus* and the impala, the alternative choice for the genus most nearly related to *Phenacotragus* falls on *Antidorcas*. The springbok agrees with *Phenacotragus* in the following skull characters.

1. The details of the shape and insertion of the male horn cores. Those of the springbok have no lateral flattened surface, are bent backwards and outwards, sometimes have the same slight tendency towards spiralization as in *P. recki*, and often have transverse ridges on their lower parts. Similar horns are found in *G. dama* of West Africa, but this species has large supraorbital pits and a long premolar row and is clearly not closely related to *Phenacotragus* or the springbok. Springbok horn cores are, however, less laterally compressed than in *Phenacotragus* or *G. wellsi*.

2. The supraorbital foramina of the springbok (Pl. 9B) and *Phenacotragus* are not set widely apart, as can be seen in Text-fig. 13 where the readings for the two genera are identical. This, combined with the high level of the frontals between the horn pedicels, gives a very similar appearance to this region of the skull.

3. The braincases of the springbok and *P. recki* are both somewhat shorter than in most gazelles. This is likely to be an advanced condition, but it has not been carried to the extreme seen in the impala.

4. In the springbok the descending flanges of the basisphenoid have their origin further back relative to the foramina ovales than in gazelles. Enough has been preserved of the fossil basioccipital piece M.22371 to show the descending flanges starting as far back as in the springbok, while in the skull M.21464 the flanges are

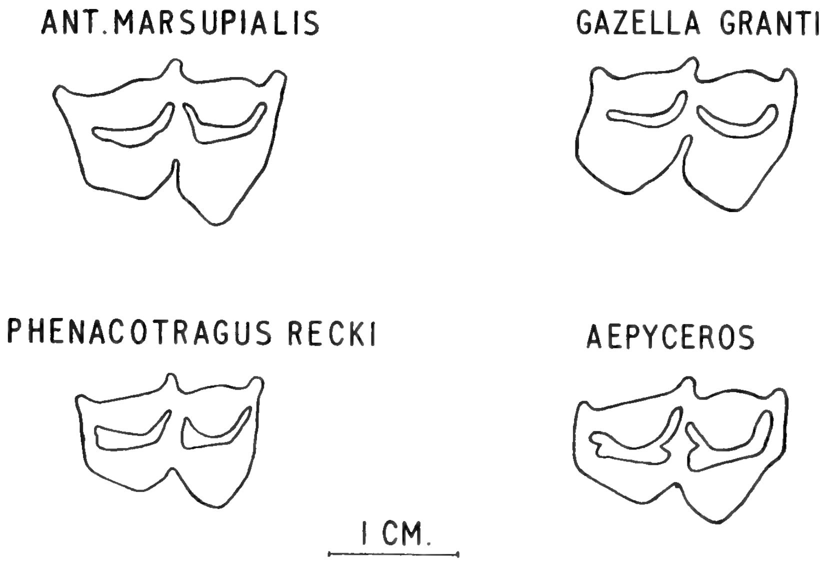


FIG. 14. Occlusal views of upper molar teeth. The lateral side is towards the top of the page and the anterior side towards the right. The *Phenacotragus* tooth is drawn from M.21464.

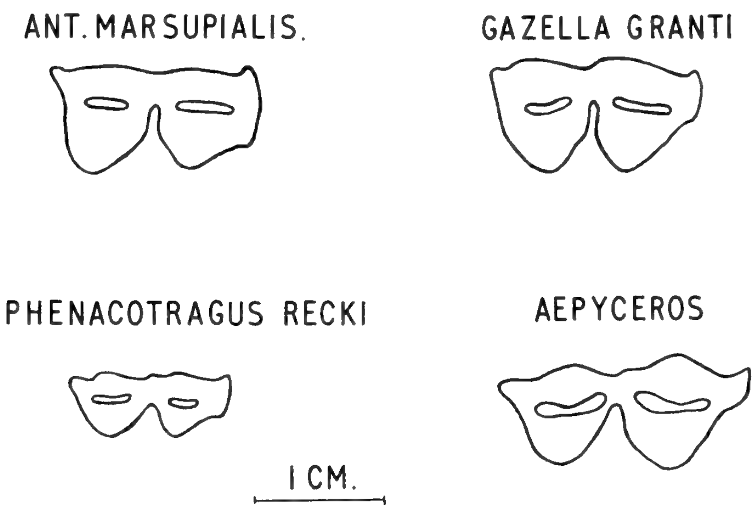


FIG. 15. Occlusal views of lower molar teeth. The medial side is towards the top of the page and the anterior side towards the right. The *Phenacotragus* tooth is drawn from M.22436.

slightly more anterior but still nearer to the springbok position than to that of gazelles ; M.21460 appears to be more like a gazelle. The basisphenoid flanges of the impala descend less sharply than in Antilopini (although the difference from M.21460 does not seem pronounced), and arise anteriorly to the foramina ovales.

5. The shape of the lower jaw's horizontal ramus in the springbok (Pl. 9C) and *Phenacotragus* is different from either gazelles or the impala. That of gazelles becomes progressively more shallow from the back forwards but there is no sharp change of direction of the lower edge as seen in profile ; males often seem to be relatively deeper under the premolars, but the difference from females was not found to be statistically significant. Passing forwards in *Phenacotragus* and the springbok the lower edge is at first very deep under the back molars, then changes direction sharply to rise under the premolars. Such a posteriorly deepened ramus is presumably necessary to house the hypsodont teeth and is dissimilar to the ramus shape of gazelles. *Phenacotragus* and the springbok also have an indentation of the lower edge of the ramus just behind the point where it changes direction. The impala has a slight bending of the course of the lower edge of its ramus, but is not so deep under the molars as in *Phenacotragus* or the springbok.

6. The lower molars of the springbok differ from gazelles in the straighter outline of their medial walls and in a more pronounced inturning of their anterior end. The central cavities are also sometimes straighter. *Phenacotragus* with the straighter medial walls of its lower molars but without such noticeably straight central cavities could easily be showing an earlier stage in the development of springbok-like teeth.

7. The upper molars of *Phenacotragus* differ from gazelles in having more prominent styles and in the more marked concavity of the posterior part of their lateral walls. The springbok is intermediate between gazelles and *Phenacotragus* in these characters. Individual teeth of the springbok could often not be told from those of gazelles, but a series from the springbok can be seen to be similar to *Phenacotragus*. (Upper molars of the impala may sometimes have a better developed mesostyle than gazelles, but only rarely have a concave posterior wall.)

8. The premolar row of *P. recki* is probably more reduced than in living gazelles, although it may not be so close to the springbok for this character as is *Gazella wellsi*. Since the impala also has a short premolar row, this character can only be used for indicating resemblance to the springbok if the other evidence for separating *Phenacotragus* from the impala is considered satisfactory.

9. A more uncertain resemblance of *P. recki* to the springbok is that in both animals the palatal foramina may be positioned rather more posteriorly than in gazelles. This is found in many individuals of the springbok and also in the cast of the type skull of *P. recki*.

10. The auditory bullae of both *P. recki* and the springbok are smaller than in gazelles or the impala. Although this may be a valid point of resemblance between them, it is also true that the size of the bulla can vary greatly, even in closely similar forms. Hence the propriety of using it here is doubtful.

It is helpful at this point to tabulate how the teeth of *Aepyceros*, *Antidorcas* and *Phenacotragus* differ.

	Aepyceros	*Phenacotragus*	*Antidorcas*
Styles on upper molars	perhaps better marked than in *Gazella*	better marked than in *Gazella*	perhaps better marked than in *Gazella*
Concave posterior part of outside wall of upper molars	rarely present	usually present	sometimes present
Tendency towards a complicated folding of the enamel walls of the central cavities of the upper molars	tendency present	less apparent	less apparent
Curvature of unworn central cavities of upper molars	better marked than in *Gazella*	as in *Gazella*	as in *Gazella*
Closed anterior valley of medial wall of P_4	present	absent	absent
Medial wall of lobes of lower molars	outwardly bowed	$\pm$ straight	$\pm$ straight
Central cavities of lower molars	constricted in the middle	as in *Gazella*	sometimes staighter than in *Gazella*
Reduction of premolars	little reduced	reduced	very reduced

The sign $\pm$ means more or less.

Few differences could be found between the skulls of *Phenacotragus* and the springbok. It is likely that the nasals of the springbok are relatively wider and that their posterior suture with the frontals has a more nearly transverse course. No complete nasal bone of *Phenacotragus* exists to provide decisive evidence on the first point, but, on the second point, the type skull, the frontlet M.21462 and the isolated nasal bone are all constant. The ethmoidal fissure of the springbok is very small or absent, being reduced at least as much as in *G. thomsoni* ; the preorbital fossa is smaller than in *Phenacotragus recki*.

The horns of springbok males are less laterally compressed than in *Phenacotragus* ; those of females are generally thin along their entire length and not greatly thickened at the base, but they are perhaps less reduced than in living gazelles, and in this they are nearer to *Phenacotragus*.

The back of the basisphenoid of *P. recki* is not so wide as in the springbok, and this is linked with the two species having dissimilar anterior tuberosities of the basioccipital. In connection with the basioccipital differences it may be noted that the cranium M.21463 (p. 58) has tuberosities not unlike either genus.

The hollow behind the maxillary flanges on the palate of *P. recki* is less deep than in the springbok.

The ascending ramus of the lower jaw of the springbok is taller than in *Phenacotragus*. In the teeth the outside wall of the posterior lobe of the upper molars in *Phenacotragus* is more concave than is usual in the springbok and the central cavities of the lower molars are not quite so straight antero-posteriorly. Both these tooth differences are minor and it should be remembered that in both genera the teeth vary in the same direction from gazelles as shown in the summary table above.

The limb bones of *Phenacotragus*, springbok and gazelles are all very much alike, and it cannot be held that *Phenacotragus* and the springbok show any closer similarities than either does to gazelles.

As there is no doubt of the close phenetic similarity of *Phenacotragus recki* to the springbok, the question arises of whether *Phenacotragus* should be dropped as a generic name in favour of *Antidorcas*. The case for this is quite strong, and in some characters *P. recki* is even suitable as an ancestor for *Antidorcas marsupialis*. Its premolar row is not so shortened as in the living species, P_2 is still present in the few available adult mandibles and P_3 is not very much reduced. The central cavities of the lower molars are not so straight as they may be in the springbok ; neither the preorbital fossa nor the ethmoidal fissure are so small. The basioccipital of *P. recki* has presumably evolved from a condition similar to that of the Pontian *Gazella capricornis*, and its anterior tuberosities could surely have evolved further to the state in which they are found in the springbok. However *P. recki* is difficult to visualize as a possible ancestor of the springbok in the characters of the outside walls of its upper molars, the shape of the back of its nasals and the horn cores of the females, but this of course need be no bar to uniting the genera.

One or two other considerations, however, suggest to me the need for caution at least for the present. Firstly there is the existence of a second species of *Phenacotragus*, namely *P. vanhoepeni* from Makapansgat in South Africa (Wells & Cooke 1956), of which there is a frontlet (M.16732) and a horn core (M.16715) in the British Museum (Natural History). Its horn cores are more massive than in *P. recki*, they seem to rise more steeply from the frontals, the lower part is longer before the horn core curves backwards and the lateral surface is flattened. They are also much more laterally compressed than in *P. recki*, and the frontals between the horn cores are not at a higher level than the orbits. The illustration of the basioccipitals shows anterior tuberosities apparently less unlike *Gazella dorcas* or *G. granti* than those of *P. recki* are. Clearly, *P. vanhoepeni* is less like the springbok than is the East African *Phenacotragus*. One could easily postulate that *P. vanhoepeni* had diverged more from the supposed central stock than had *P. recki*, but this is to wander away from available evidence.

Secondly there is the appearance of characters reminiscent of *Antidorcas* in other fossil gazelline species at Olduvai. In *G. wellsi* the supraorbital pits are very small and the frontals between the horn bases are at a higher level than the orbital rims, the horn cores are bent backwards, the premolar rows are shorter than in living gazelles and P_2 is even sometimes absent. The gazelline cranium (M.21463), which was a surface find from FLK II in 1935 (see p. 58), is not distinguishable from the *G. wellsi* of Bed I, and has a basioccipital which is morphologically intermediate between *Phenacotragus* and *Antidorcas*. Among the limb bones from the 1960 excavations the slight vertical ridge on the anterior surface of the femur FLKN I, 1027 is the most striking springbok-like character.

Several explanations are possible for these phenomena and it is evident that the phyletic relationships between the springbok, the two species of *Phenacotragus*,

Gazella wellsi and other gazelles are not yet clear. It is advisable to consider what may be the far-reaching implications of some of the skull characters of these East African fossils. It is particularly characteristic of the genus *Gazella*, as far back as in the Pontian species of Attica, to have a low level of the frontals between the horn cores' bases. This condition is also found in the related genera *Oioceros*, *Helicotragus*, *Antilope*, *Litocranius* and *Ammodorcas*, and in some Bovid tribes other than the Antilopini, e.g. the Neotragini and Reduncini. *Antidorcas*, *Gazella wellsi*, *Phenacotragus recki* but not *P. vanhoepeni* show the opposite condition of high level frontals coupled with supraorbital pits which are either small or absent, and which even when present lack the characteristic gazelline triangular shape. Such characters do not occur in Eurasian fossil gazelles or even in those described from the Algerian upper Pleistocene.

If the African forms are descended from typical gazelles, then their high frontals and small supraorbital pits are a relatively late evolution, and they might best be classified by retaining *G. wellsi* within *Gazella*, and by separating the other two as *Antidorcas* and *Phenacotragus* if they are two different and parallel divergences from this stock, or by putting them both in *Antidorcas* if they are the products of only one such divergence. But it is still not known even that the two *Phenacotragus* species are closer to one another than to the other forms, nor can it be assumed that *Gazella wellsi* is phenetically or phyletically further from the springbok than *Phenacotragus* is.

If, on the other hand, the Pliocene and earlier ancestors of these African forms also possessed high frontals and small non-triangular supraorbital pits, their relationship to typical *Gazella* is more distant. It may well be that a predominantly grazing "Antidorcine" group of Antilopini has long inhabited Africa, existing alongside typical gazelles such as are represented at Olduvai by the horn cores SHK II 285, BK II 226 and M.14508 (see above), and that the springbok of South Africa is the only survivor of this formerly more widespread and diverse stock. Further finds at Olduvai and at other East African sites may give more information about this interesting possibility. If evidence were found in support of it, then the problem of classification might be dealt with by placing *G. wellsi*, *Phenacotragus* and *A. marsupialis* all in the genus *Antidorcas*.

A third still more hypothetical possibility is that the springbok, *Phenacotragus* species and *G. wellsi* are a gazelline-like development from the hartebeest group—a possibility which would much weaken the idea of even a remote relationship of the hartebeest group to the gazelline-caprine stock. If it were true the problems of generic differentiation would remain, but within a different tribe. In the absence of evidence for one of these three evolutionary histories, it is best to retain the existing name *Phenacotragus* and to refrain from moving *G. wellsi* to another genus. Under this arrangement the genus *Phenacotragus* differs from *Gazella wellsi* by having horn cores which are longer, less divergent proximally but outwardly divergent in their distal parts, and a concave outer wall of the posterior lobe of the upper molars. The flattened lateral surface of the horn cores, available as a character in East Africa to distinguish *P. recki* from *G. wellsi*, is not available in this broader context because of the flattened lateral surface of *P. vanhoepeni* horn cores.

It may be useful at this point to summarize the contrasts in skull evolution in *Phenacotragus*, *Antidorcas* and "normal" gazelles. *P. recki* and *Antidorcas* have a high level of the frontals between the horn bases and small supraorbital pits, and the descending flanges of the basisphenoid originate more posteriorly relative to the foramina ovales. They are advanced from Pontian gazelles in having shortened braincases (but note the less marked tendency towards shorter braincases in *Gazella rufifrons* and *G. soemmerringi*), better developed styles on the upper molars, straighter medial walls of the lower molars, the posterior deepening of the mandible, and the reduced premolar row. But they have retained rather long nasals, they have little transverse compression of the horn cores, and the horn cores of females are often less reduced than in gazelles.

The living African gazelle which shows the most extreme differences from the springbok and *Phenacotragus* is *G. thomsoni*. Admittedly *G. thomsoni* has a reduced premolar row, but even here there is slender evidence (Gentry 1964) for supposing that *G. thomsoni* reduces the back of its premolar row rather than P_2.

Some of the skull characters of *Gazella wellsi*, *Phenacotragus* and *Antidorcas* in Africa are paralleled in the Caprinae of Eurasia. Such characters are the shorter braincase than in most gazelles, the high level of the frontals and the strong development of the central anterior flanges of the nasals, which are all carried to a further extreme in *Capra* and *Ovis*. The shallowness of the mandible under the premolars in *Antidorcas* and *Phenacotragus*, the development of the styles on the upper molars of *Phenacotragus*, and the possibly prominent metastyle of M^3 in *G. wellsi* are also approaches to the caprine condition. P_2 has disappeared in *Saiga* on the steppes of Asia as in the African species, but the advanced structure of P_4, found in the *Procapra* group and Caprinae, is unknown in any African gazelline species.

VII. SUMMARY AND CONCLUSIONS ABOUT THE GAZELLINE FAUNA OF OLDUVAI

The introduction to this work contains revised definitions of the Antilopini, *Gazella* and *Antidorcas marsupialis*, together with a discussion of some tooth characters of gazelles. The remainder is about the gazelline fauna of Beds I and II at Olduvai so far as it is known, and the chief point of interest is its marked difference from the fauna now living in East Africa. Today there are the smaller *Gazella thomsoni*, the larger *G. granti*, and *Litocranius*; then there were *G. wellsi*, *Phenacotragus recki* and several others.

Phenacotragus recki is more nearly related to the extant South African springbok than to present day East African forms, as is shown by the shape and insertion of the horn cores, the size of the supraorbital foramina, the high level of the frontals between the horn bases, the short braincase, the probably rearward position of the descending flange of the basisphenoid, the shape of the mandible, and by certain details of tooth structure and proportion.

Gazella wellsi similarly shows certain resemblances to the springbok, and until the relations between this form, *P. recki*, the South African fossil *P. vanhoepeni* and the

springbok can be seen more clearly it is inadvisable to alter the existing formal nomenclature.

While *P. recki* and *G. wellsi* appear from their advanced teeth to have been predominantly grazing forms, there are a further three or more gazelline species from Olduvai, which may have included browsing forms. They are incompletely preserved, and at least two of them appear to belong to *Gazella*. Only the horn core (M.14508) is at all like the living species. It is not yet clear how many of the fossil species would have occurred together at any one time.

P. recki does not appear to have any convincing resemblances to the impala, although Schwarz (1937) thought that it did, and I believe that the genus *Aepyceros* should be removed from the Antilopini and added to the Alcelaphini.

The gazelline limb bones from Bed I show less fully cursorial proportions than in any comparable living African form.

There are no fossil remains referable or related to *Litocranius*, and none shows such brachyodont teeth or such a shallow jaw ramus. The ancestry of *Litocranius* is unknown, it is so specialized in several respects for browsing that it may have come from less brachyodont ancestors.

There are no recognizable remains at Olduvai of the spiral-horned genera of the *Helicotragus-Antilope* group. The nearest record is at Bethlehem where Hooijer (1958) has found *Gazellospira torticornis*.

APPENDIX I

The method of referring teeth to certain age states which has been followed in this paper is that of Brooks (1961 : 132) ; his definitions of the relevant age states are :

- VII. Milk premolars lost ; permanent premolars fully erupted but not worn ; third molar fully erupted.
- VIII. First molar slightly worn, still with centre crest and sulci deeply cleft and V-shaped.
- IX. First molar without centre crest, sulci crescent shaped ; third molar crested with V-shaped sulci.
- X. First molar worn, surface smooth with no vestige of sulci ; third molar moderately worn, with crescent shaped sulci.

Measurements mentioned in this paper were taken on all suitable fossils, and on Recent specimens in age states VIII and IX as defined immediately above, that is on young adults. The measurements were :

antero-posterior diameter of horn pedicel . . . the longest dimension of the pedicel, irrespective of whether it was parallel to the long axis of the skull ;

transverse diameter of the horn pedicel . . . the measurement at right angles to the antero-posterior diameter. These first two dimensions were taken on the pedicels rather than the horn cores because the sheaths of Recent species in museum collections are often irremovable ;

length M^1–M^3 . . . . the maximum length at crown level ;
length M^2 . . . . the maximum length at crown level ;
length P^2–P^4 . . . . from the centre of the posterior wall of P^4 to the anterior wall of P^2, irrespective of whether the occlusional surface extends as far as the anteriormost point ;
length P^2 . . . . from the centre of its posterior wall to the anterior wall, irrespective of whether the occlusional surface extends as far as the anteriormost point ;
parieto-occipital angle . . measured with a carpenters' sliding bevel ;
braincase width . . . . the widest possible dimension ;
orbital width . . . . the widest possible measurement across the posterior side of the orbits ;
separation of horn cores . the distance apart of the closest points of the lateral sides of the horn pedicels ;
separation of supraorbital foramina . . . taken between the central points of the lateral walls.

The measurements on the fossils, expressed in centimetres unless otherwise stated, were :

Phenacotragus recki (Schwarz)	Age state	Antero-posterior diam. of horn pedicel	Transverse diam. of horn pedicel	Length M^1–M^3	Length M^2	Length P^2–P^4	Length P^2
M.21460	IX	3·72	2·58	4·03	1·43	2·39	0·77
M.21462	—	3·26	2·34	—	—	—	—
M.21464	VII	2·85	2·14	3·71	1·45	c2·06	—
1960, FLKN I, 627	VIII	—	—	3·83	1·38	1·85	0·53
Gazella wellsi Cooke							
1960, FLKN I, 6334	X	2·85*	2·12*	c3·73	1·26	c1·87	0·55
1960, FLKN I, 1152	IX	—	—	3·72	1·27	1·79	0·57
1960, FLKN I, 1662	X	—	—	4·62	1·56	2·27	0·75

* Not used in the histogram on Text-fig. 8.

Other horn cores placed with *Gazella wellsi* had the following dimensions :

1960, FLK I, G.13, 229	3·02×2·19	1941, F.944	2·92×2·14
M.22360	3·61×2·25	M.22363	3·18×2·38
1941, F.939	3·43×2·71	1941, F.940	3·08×2·15

Those of group (A) measured :

1959, KK I, 309	3·03×1·91	M.14512	2·87×1·88
1959, HWK II, 472	2·33×1·56 (the supposed female).		

1953, SHK II, 285 in *Gazella* species of group (B) measured 2·82×2·31.
M.14508, group (F), measured 2·64×2·00.

Other measurements of length of M²s in specimens assigned to *Gazella wellsi* were 1·16, 1·23, 1·10 and 1·30. 1960, FLKN I, 122, placed with *Phenacotragus recki*, is a molar tooth 1·54 cm. long ; it is assumed to be an M².

Other measurements on the skulls of *P. recki* were :

	Parieto-occipital angle	Braincase width	Orbital width	Separation of horn cores	Separation of supra-orbital foramina
M.21460	132°	6·45	9·46	—	2·98
M.21462	—	—	c9·20	6·13	3·00
M.21464	132°	c5·17	8·52	5·90	3·06

Measurements of length and least thickness were taken on limb bones of the following species :

	Males	Females	Sex unknown	Young or juvenile
Aepyceros melampus	3	2	–	2 (male and female)
Antidorcas marsupialis	1	1	–	–
Gazella dorcas	1	–	2	–
Gazella thomsoni	3	2	1	1 (male)
Gazella granti	6	4	1	–

The readings for young animals have not been entered on the histograms in Text-figs. 9, 10 ; they had relatively longer metapodials and shorter radii and tibiae than the adults. All the front leg bones were thinner than in adults except for the radius of the juvenile *G. thomsoni*, but in the back legs the differences from adults were less marked and not reliable.

The lengths of the limb bones were measured as follows :

femur : from the lateral end of the articular head to the ventralmost level of the posterior part of the medial condyle ;

tibia : from the ventralmost point of the medial facet at the top to the posterior tip of the bone behind the medial malleolus ;

metatarsal : from the highest point of the bone behind the ectocuneiform facet medially to the articular surface on the medial side of the most projecting part of the medial condyle distally ;

humerus : from the top of the greater tuberosity to the ventralmost point of the medial side distally ;

radius : from the medialmost point of the medial facet to the most distal point of the ridge bounding the scaphoid facet medially ;

metacarpal : from the anterior edge of the articular facet at the extensor carpi radialis insertion to the articular surface on the median side of the most projecting part of the medial condyle distally.

APPENDIX II

Excavations at Laetolil near Olduvai in 1935 and 1959 have yielded fragments of apparently gazelline horn cores and teeth, most of which differ from Olduvai remains. Specimens M.22483, three of M.22484, M.22491 and M.22494 are horn cores of almost circular cross section, two specimens numbered M.22484 are smaller than the others and may be females ; it may be that these Laetolil finds represent large Neotragini, but two left horn cores in Nairobi, 1959, 46 and 50, are more like a small species of *Gazella.* M.15110, M.22485, two of M.22486, two of M.22487, three of M.22488, M.22492 and M.22495 are all mandible fragments which are very shallow below the teeth ; 1959, 298 and 603 at Nairobi are also of this group. The distal end of humerus (M.22489) may go with the largest group of horn cores and mandibles, as may also two astragali, 1959, 19 and 328 at the National Museum in Nairobi. These astragali, together with Olduvai, 1959, MTK I, 104 have a shallow excavation on the lower part of the lateral side.

Also from Laetolil is a mandible fragment, 1959, 54, which has a deeper ramus than those mentioned above, although its teeth seem identical. A large gazelline species is represented by 1959, 150, 151, 294 and 443 + 444 and by one of the pieces numbered M.22487 in the British Museum (Natural History). These are all mandible fragments or lower teeth, perhaps from a large species of *Phenacotragus* judging by the relatively straight medial walls of the teeth.

The 1964 excavations at Lake Natron have revealed fragments of a large *Phenacotragus* represented by the maxilla WN 64, 300B, and a small *Phenacotragus* represented by the horn cores WN 64, 113, the mandibles WN 64, 95, 152, 241 and 291, and possibly by the limb bones WN 64, 79 and 213. Also from the Lake Natron beds are the horn cores WN 64, 75 and 126 which might be the same as the Laetolil *Gazella* 1959, 46 and 50. Isaac (1965) gives details of the Natron beds.

A gazelline horn core (M.15883) from Kanam West is like M.14508 from Olduvai (p. 67) in size and in its index of lateral compression at 76 (see Text-fig. 8). It differs from M.14508 in having a narrower section anteriorly, that is by having its level of maximum width further back and more localized ; this may be a slight feature morphologically but it does give M.15883 an appearance very like that of modern gazelles. In their three characters of size, lateral compression, and shape of cross-section, the two fossil horn cores agree with *G. rufifrons* among living species.

Those of *G. dorcas* are smaller and have the level of maximum width still further back ; in *G. spekei* they are smaller and have pronounced lateral compression ; those of *G. thomsoni* are nearer in size but again have much lateral compression ; while those of *G. rufifrons* are similar in size and shape and are only slightly more compressed. Without more finds of this fossil animal, one cannot know whether it is related to a living gazelle or whether the resemblances to *G. rufifrons* are a matter of chance.

Two horn cores from Kanjera (M.15851) and one from Aringo Karungu (M.22502) are very like *G. granti* in both size and extent of lateral compression.

APPENDIX III

Leakey (1965) has given a preliminary report on the Olduvai gazelline species. He considers that Schwarz's species *Gazella gazella praecursor* may be represented in the British Museum's Olduvai collection by the horn cores M.14507 and M.14508 on account of their likeness to *G. thomsoni*—the species to which *G. g. praecursor* was supposed to be the forerunner. I have placed M.14507 with the *Gazella* species (B) of this paper but agree that M.14508 is similar to *G. thomsoni* despite its having less transverse compression than that species.

Leakey's species (a), the 1935 herd excavated from SHK II, is also here taken to be *Phenacotragus*, and I have been unable to separate it satisfactorily from *P. recki*.

The horn core (b) which is said to have " certain resemblances to the horn cores of the so-called ' Mongolian gazelle ' ", I believe to belong to a small *Damaliscus* or to a genus closely related to *Damaliscus*.

(c) The horn core (M.14513) is one of those which I have determined, perhaps rashly, to be females of *Phenacotragus* as explained earlier in this paper. Leakey's description of his species (c) fits the horn cores belonging to group (A) of this paper, one of which is numbered M.14512.

(d) The skull figured by Leakey (1965, pl. 85) is M.21463, a surface find from FLK II which seems to be *G. wellsi*.

(f) The frontlet 1955 BK II East, surface find no. 7 is a lightly fossilized young *G. granti*, or *G.* cf. *granti* according to Leakey. The entry in the record of excavations for 1955 reads : " Pair of horn cores and frontlets, surface above Bed III ? from V on condition. in two parts ". From this it seems unlikely that the frontlet belongs to a Bed II fauna.

The specimens listed under the headings (g), (h) and (i) are all taken here as belonging to *G. wellsi*, and have been considered earlier in the paper.

(j) The horn cores figured by Leakey (1965, pl. 86) might be Antilopini as he suggests, but more complete remains of such surprising animals are needed for a reliable assignation.

The horn core (M.14563) which Leakey (1965 : 65) records as *Phenacotragus recki* is here taken to be a later occurrence of *G. wellsi*.

The impala-like horn core 1957, BK II, 662 mentioned by Leakey also seems to me good evidence of the presence of *Aepyceros* in upper Bed II.

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PLATE 1

Gazella wellsi Cooke

(Scales represent 1 cm.)

A. Lateral view of the horn core 1960, FLKN I, 1307.

B. Parts of the skull 1960, FLKN I, 6334; note the preorbital fossa on the right maxilla.

C. Maxilla 1960, FLKN I, 1152, below; maxilla 1960, FLKN I, 1662 is shown above for comparison.

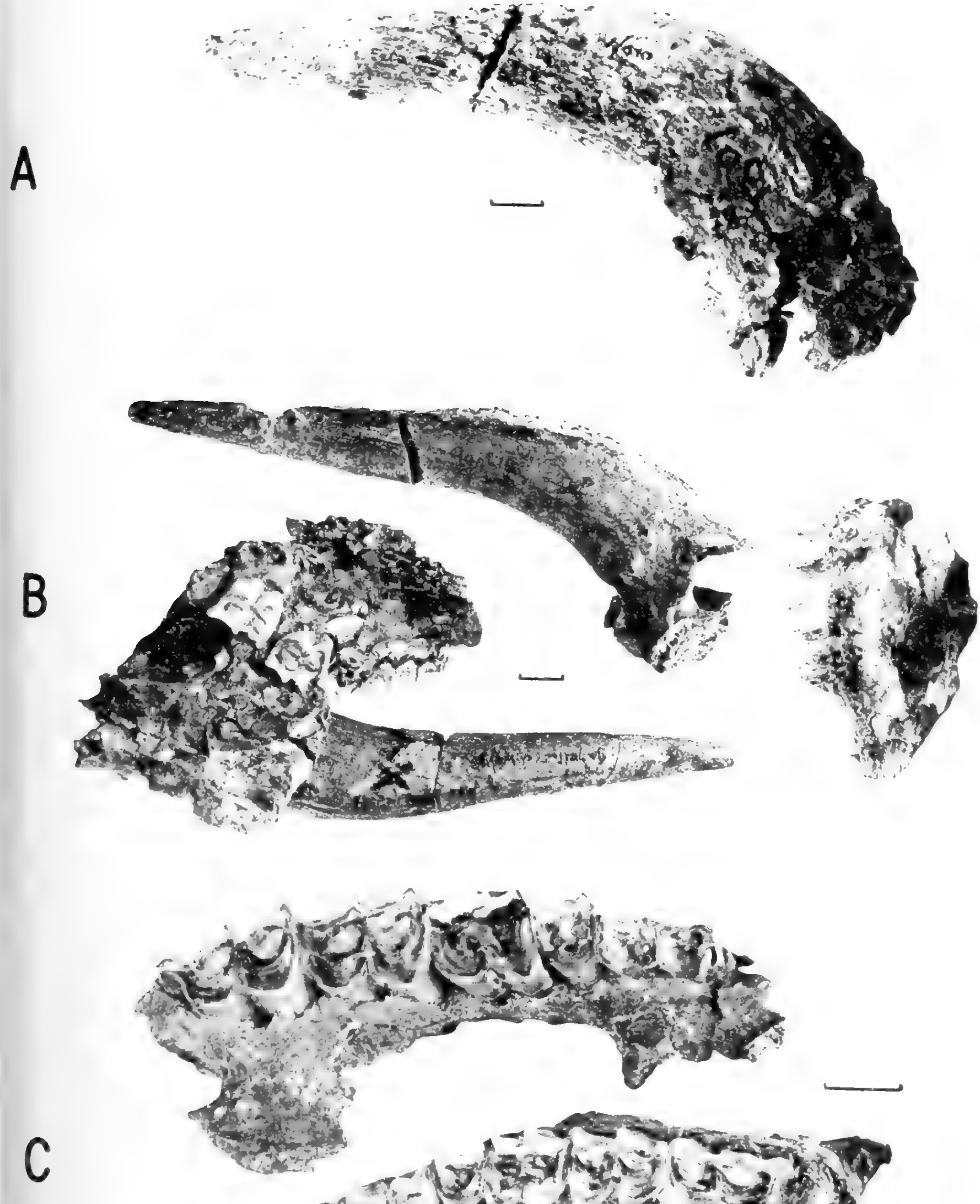

A
B
C

PLATE 2

(Scales represent 1 cm.)

A. ***Gazella wellsi*** Cooke. Lateral view of mandible 1960, FLK I, G.323.

B. ***Gazella wellsi*** Cooke. Lateral view of mandible 1960, FLK I, G.294 ; only two premolars are present.

C. Left : gazelline species of Group (A), medial view of horn core 1959, KK I, 309. Right : ***Gazella*** species of group (B), lateral view of horn core 1953, SHK II, 285.

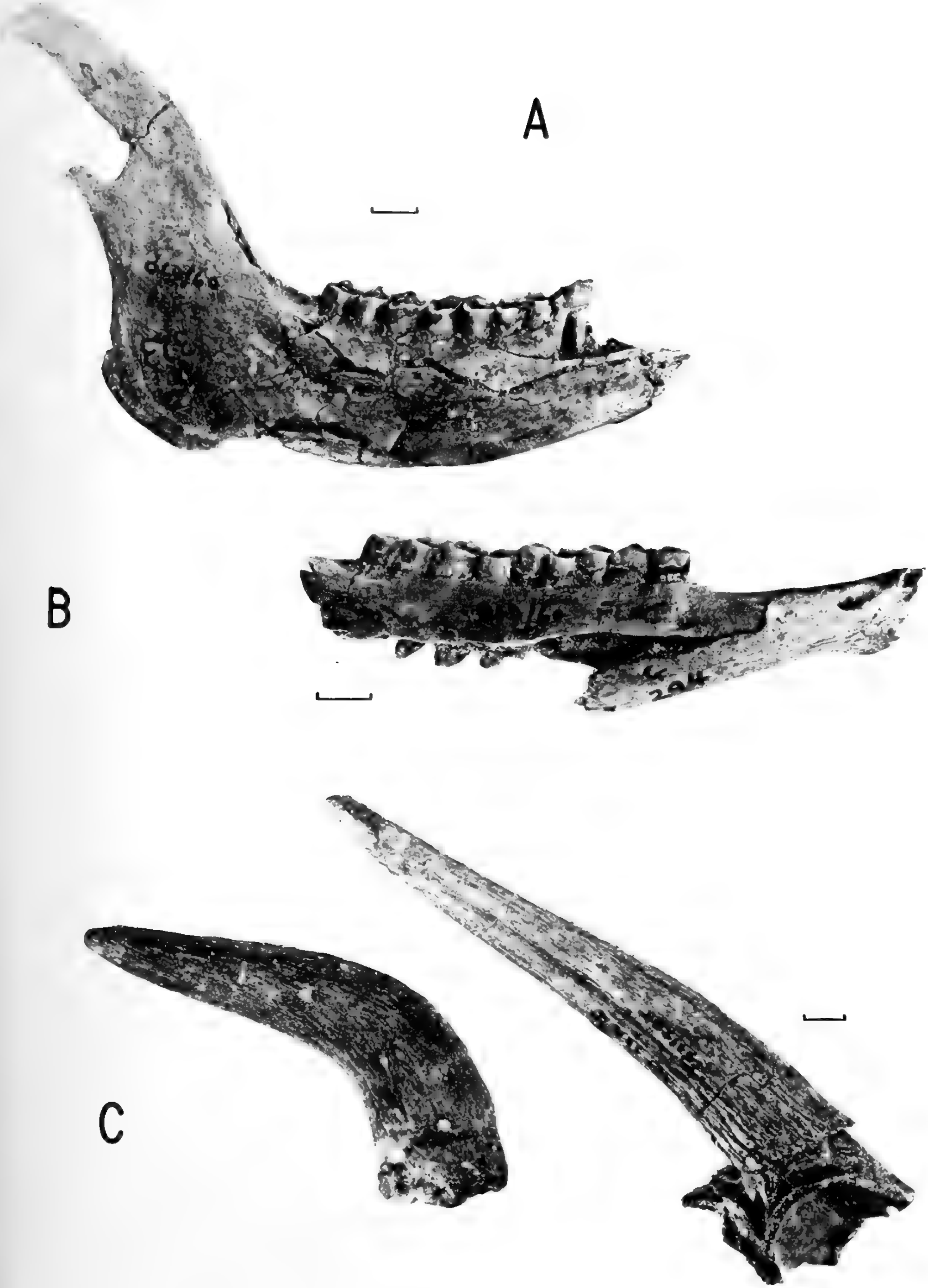

A
B
C

PLATE 3

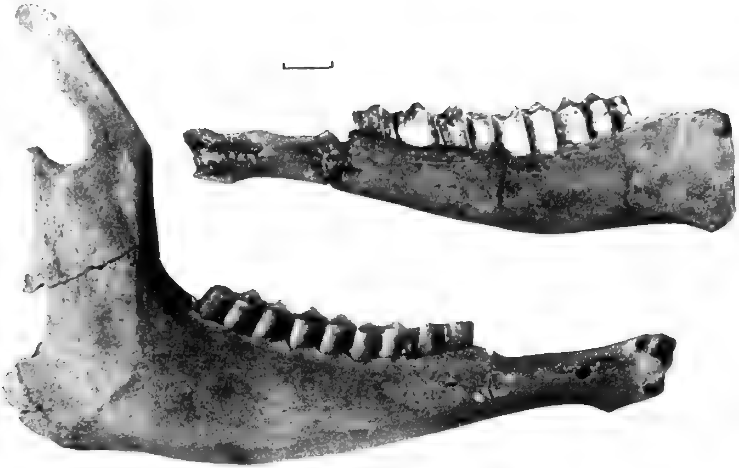
(Scales represent 1 cm.)

A. Above : lateral view of mandible 1957, SHK II, 793,—group (C). Below : lateral view of mandible, M.22379,—group (D).

B. Lateral view of mandible 1960, FLKN I, 1293, and occlusal view of lower teeth 1941, Bed I, F.109. Group (E) in the text.

C. Lateral view of horn core, M.14508. Group (F) in the text.

A



B

C

PLATE 4

(Scales represent 1 cm.)

A. Anterior views of proximal ends of femora. ***Antidorcas marsupialis*** (Zimmermann) on the left, and 1960, FLKN I, 1027 on the right. Both have a slight vertical ridge below the hollow between the articular head and the great trochanter.

B. Lateral views of tibiae. Male ***Gazella thomsoni*** Günther above and 1960, FLK I, F.161 below. Notice the curving of the axis of the fossil tibia.

C. Anterior views of radii. Male ***Gazella thomsoni*** Günther above and 1960, FLKN I, 682 below. The fossil bone is thicker and shorter.

A

B

C

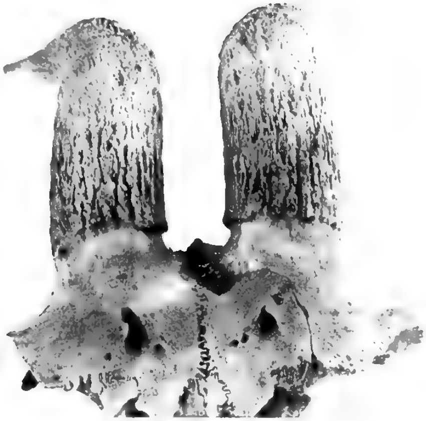
PLATE 5

Phenacotragus recki (Schwarz)

A, B. Anterior and lateral views of frontlet, M.21462. The distance between the supraorbital foramina is 3·0 cm.

C, D. Anterior and lateral views of cranium, M.21464. The distance between the supraorbital foramina is 3·1 cm.

A



B

C

D

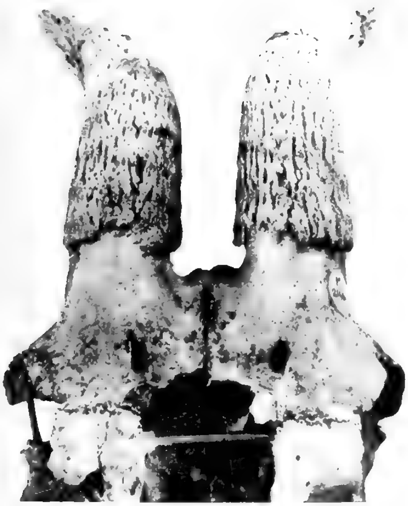


PLATE 6

Phenacotragus recki (Schwarz)

A, B. Anterior and lateral views of the cast of the type skull, M.21460.

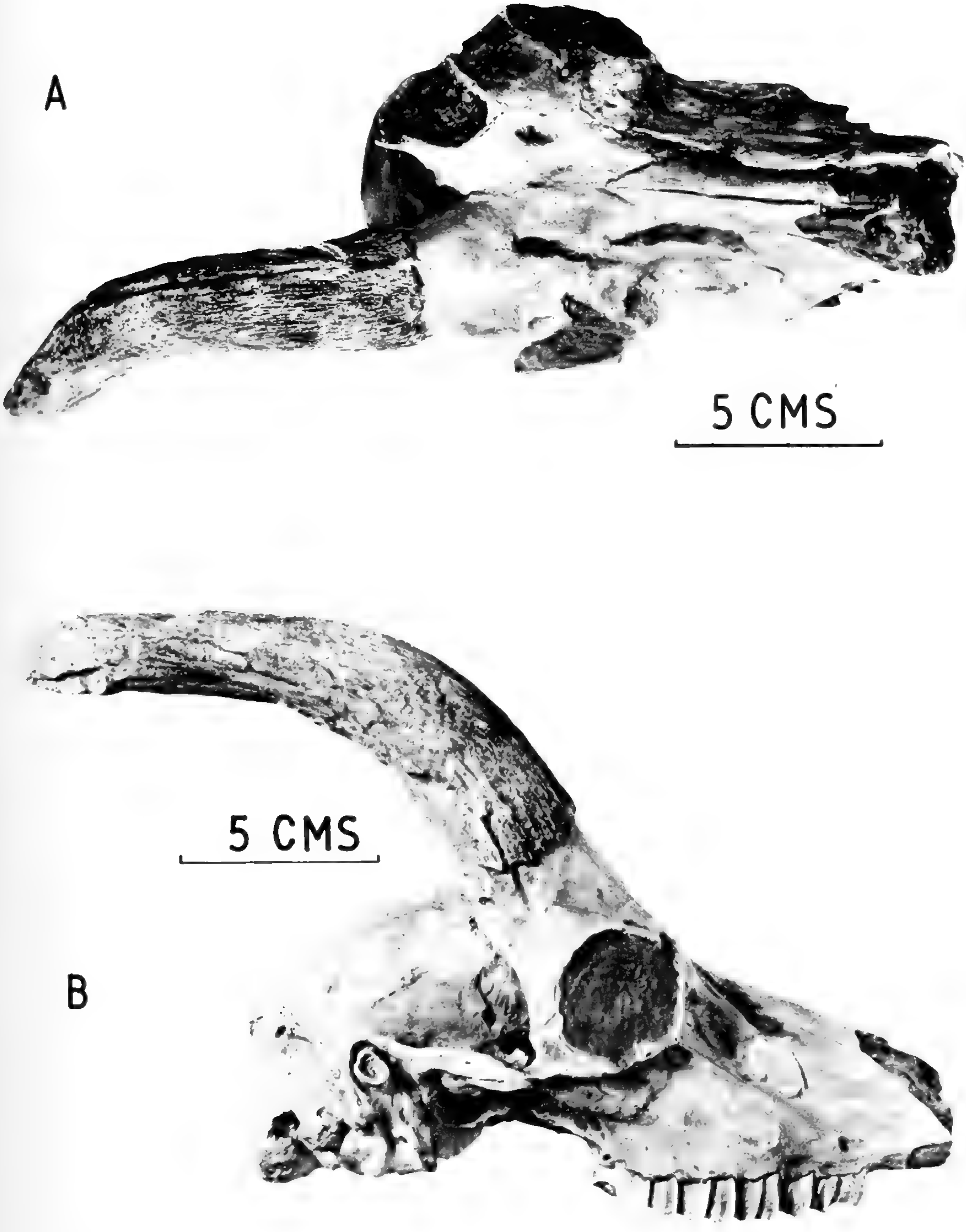

A
5 CMS
5 CMS
B

PLATE 7

Phenacotragus recki (Schwarz)

(Scales represent 1 cm.)

A. Two horn cores supposedly female, M.14513 (left) and 1960, FLKN I, layer 5, no number (centre), compared with a female horn core (M.22362), perhaps belonging to the *Gazella* species of group (B).

B. Basioccipital, M.22371. The descending flanges of the basisphenoid can be seen antero-externally to the anterior tuberosities on the left of the picture.

C. Upper teeth of the skull, M.21464.

A

B

C

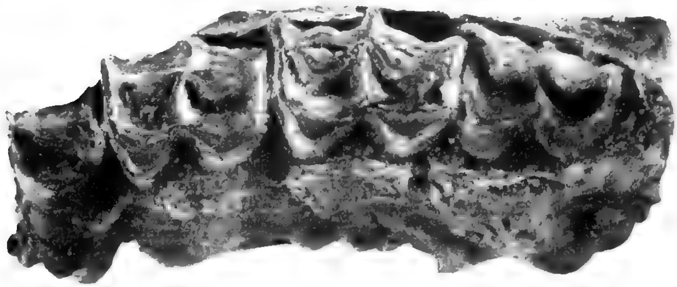


PLATE 8

Phenacotragus recki (Schwarz)

(Scales represent 1 cm.)

A. Lateral view of the left mandible, M.22436; note the small P_2, low ascending ramus of the mandible, and alteration of the course of the lower edge of the mandible at the level of M_2.

B. Anterior view of bones of back leg; sub-adult individual.

C. Anterior view of bones of front leg; fully adult individual.

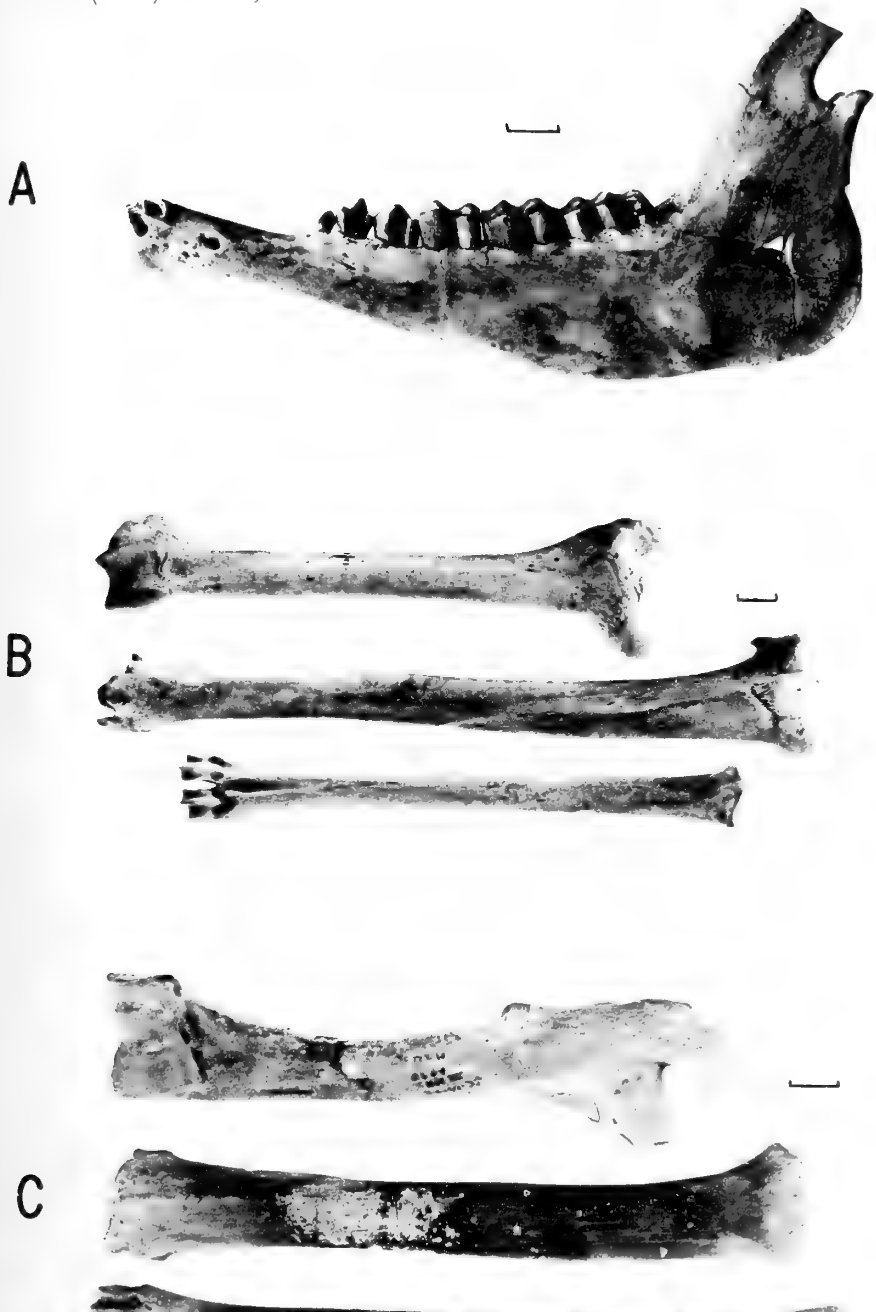

A
B
C

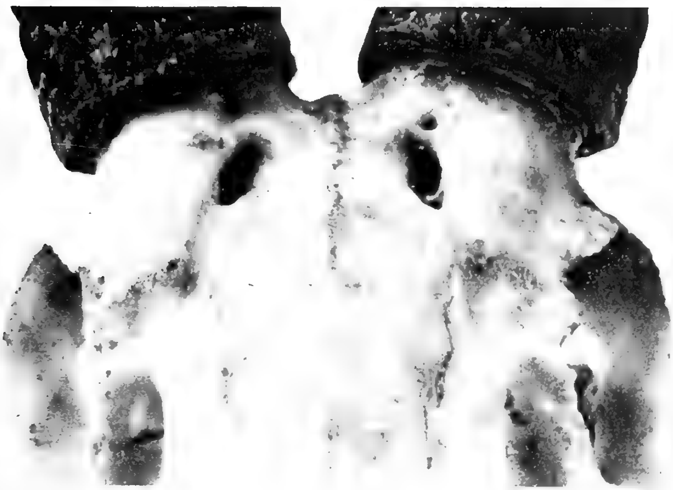
PLATE 9

A. ***Gazella dorcas*** (left) and ***G. thomsoni*** Günther (right). Anterior view of the frontlets.

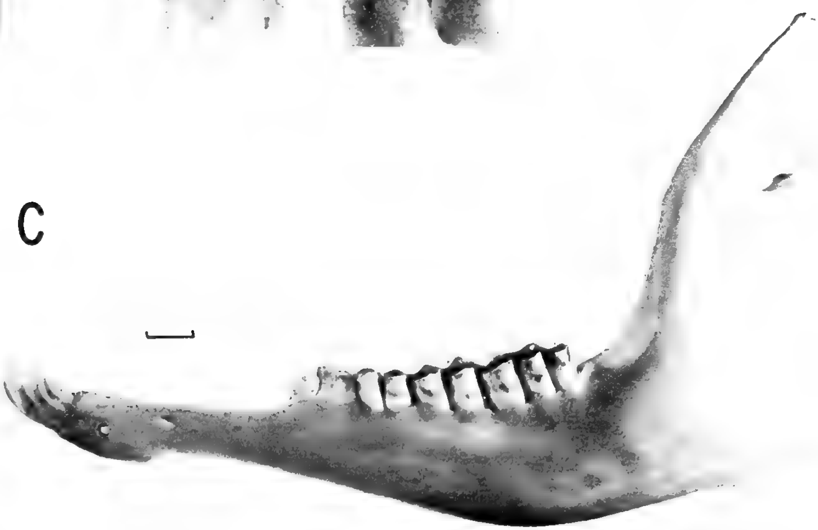
B. ***Antidorcas marsupialis*** (Zimmermann). Anterior view of skull to show the high level of the frontals between the horn bases, and the small supraorbital pits.

C. ***Antidorcas marsupialis*** (Zimmermann). Lateral view of lower jaw ; its lower edge shows an abrupt change in direction below the junction of M_2 and M_3. Scale represents 1 cm.

A



B



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THE FAUNA OF THE PORTRANE LIMESTONE, IV: POLYZOA

BRITISH MUSEUM NATURAL HISTORY

J. R. P. PHILLIPS ROSS

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THE BRITISH MUSEUM (NATURAL HISTORY)
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LONDON: 1966

THE FAUNA OF THE PORTRANE LIMESTONE, IV
POLYZOA

BY

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(Department of Geology, University of Illinois, U.S.A.)

Pp. 107–135 ; 8 *Plates*

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THE FAUNA OF THE PORTRANE LIMESTONE, IV: POLYZOA

By J. R. P. PHILLIPS ROSS*

CONTENTS

SYNOPSIS

In the Portrane Limestone the Orders Trepostomata, Cryptostomata and Cyclostomata are represented by 19 genera and 26 species which comprise a very distinct fauna dominated by delicate cryptostomes. The trepostome *Anaphragma* is represented by a new species, *A. potranense*. *Mitoclemella?* sp. A is a very significant cryptostome occurrence because the genus

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Mitoclemella has only been previously recorded from the Prosser Formation, Minnesota, and the C_2 horizon of Estonia. An unusual polyzoan with a cup-like form is another early representative of the cyclostome family Diastoporidae and appears closely similar to the Cretaceous genus *Discosparsa*.

I. INTRODUCTION

THIS investigation of the Polyzoa[1] is part of a study by several palaeontologists examining the fauna of the Portrane Limestone. Wright (1963), who collected and etched large blocks of the Portrane Limestone, has discussed and outlined the stratigraphic sequence and the proposed description of the Upper Ordovician fauna.

The polyzoans from the Portrane Limestone are variously preserved: (1) some colonies are partly silicified; (2) others have recrystallized calcareous skeletal structures; and (3) yet others are well preserved calcareous colonies. The very careful etching and processing of the etched material by Dr. Wright resulted in the recovery of many minute and delicate fragments of cryptostome and cyclostome polyzoans. These fragments present much data on the morphology of some of the species that otherwise would be impossible to assemble from thin sections because the colonies were extensively fragmented during the deposition of the Portrane Limestone. The etched trepostome colonies generally are considerably larger in diameter than the cryptostomes and their surfaces are commonly completely silicified so that external surface features of the zoaria can be readily observed. However, the internal structures of these trepostomes are very incompletely preserved and the material is not suitable for thin sectioning. The thin sections of the cryptostomes and trepostomes were made from random cuts through blocks of polyzoan-bearing limestone. However, very extensive thin sectioning has not revealed all the minute cryptostomes and cyclostomes that are preserved in the etched material.

Identifying the Portrane material has involved a number of difficulties, largely due to two factors. First, the small, etched fragments commonly do not permit complete description of a species because information about the general aspects of a colony and its internal structures are not determinable. Secondly, the early literature which described many of the forms similar to the Portrane fauna commonly does not present a detailed discussion of the species and genera and only a limited amount of data can be obtained from the published illustrations.

The Portrane polyzoans are represented by at least 19 genera and 26 species. Many of the genera such as *Enallopora*, *Mitoclemella* and *Anaphragma* are distinctive forms and this profusion of different forms at one locality is similar to the abundant faunas found in the Estonian late Ordovician and in parts of the Cincinnatian of the United States. Portrane is a locality intermediate between these two regions and it contains many polyzoan genera common to the North American and Baltic areas. At the species level, the Portrane assemblage has little similarity with that of either the United States or Estonia.

The species offer no refined data about the age of the Portrane Limestone at the present time because of the many gaps in our knowledge of Ordovician polyzoan

[1] Polyzoa is used in the text in conformity with the usage of the Museum.

distributions. *Anaphragma portranense* has little similarity with the few species so far attributed to this genus from either the Cincinnatian, Wilmington, Illinois, or the F_1 horizon in Estonia. *Calopora* sp. A belongs to a group which includes the type species of *Calopora* and which ranges from Trentonian to Niagaran in the United States. *Amplexopora* sp. appears to belong to the group of typical species of *Amplexopora*, the type species occurring in the " Cincinnati Group ", Ohio and Kentucky. *Enallopora* sp. A has similarities with species from the Trentonian of New York State, Cincinnatian at Wilmington, Illinois, and the D_1 to F_{1c} horizons of Estonia. *Mitoclemella?* sp. A is a distinct form showing similarity with the type species of *Mitoclemella* from the " Trenton ", Minnesota, U.S.A., whereas the species of *Penniretepora* show no close similarities. *Pseudohornera?* sp. A has some similarity with a species from the C_3 horizon of Estonia. A very slender species of *Ptilodictya*, *Ptilodictya* sp. A, has similarities with *P. ensiformis* which ranges from the Cincinnatian to Niagaran, Anticosti Island. A more robust species, *Ptilodictya* sp. B, belongs to a group which includes the type species, *P. lanceolata*, and *P. canadensis*.

Only broad correlation between the Portrane and Estonian faunas based on the genera is at present possible because much additional data on Ordovician polyzoan faunas in many regions has yet to be compiled. In the Estonian succession Männil (1959, 1962) has documented the occurrence of many of the genera which are also found in the Portrane fauna. Männil (1959 : 38) recorded *Ptilodictya* as extending down to the F_{1a} horizon, but (1962) modified this range so that the genus is now considered to extend down into the D horizon ; it extends upwards into the Silurian. Männil (1959, 1962) indicated that *Glauconomella* extended from F_{1a} into the Silurian. Depending on the redefinition of *Glauconomella*, some of the Portrane forms assigned to *Penniretepora* in the present study may belong to *Glauconomella*. *Stictopora* is known from the C_{1b} horizon and extends upwards ; *Pachydictya*, *Nematopora*, and *Calopora* are first recorded in the C_{1a} horizon ; *Anaphragma* extends from the D_2 to F_{1b} horizons, and *Dianulites* from the B_2 into at least the F_2 horizon ; *Enallopora* and *Pseudohornera* occur in C_{1b}, and *Mitoclemella* was recorded by Bassler (1911) from the C_2 horizon.

The Portrane polyzoan fauna, based on comparisons with the present incomplete faunal data from other regions, could be as old as faunas from the D horizon of the Estonian succession and as young as those from the F_2 horizon in the Estonian succession.

II. SYSTEMATIC DESCRIPTIONS

Order TREPOSTOMATA Ulrich

Genus *ANAPHRAGMA* Ulrich & Bassler

Anaphragma portranense sp. nov.

(Pl. 1, figs. 1, 2, 4, 6 ; ? Pl. 6, figs. 4, 6)

DIAGNOSIS. *Anaphragma* with slender branches having large zooecial openings, numerous small acanthopores which penetrate the junctions of zooecial walls and mesopore walls, and numerous mesopores.

MATERIAL. Holotype PD.4390, paratype PD.4391. Questionably assigned to the species, PD.4425, PD.4432.

DESCRIPTION. Slender zoarial branches are circular in transverse section. Well defined axial regions shows slender irregularly crenulate zooecial walls which thicken as they pass into the peripheral region. In longitudinal section zooecial walls in the peripheral region have steeply inclined laminae in their inner parts; these laminae curve sharply and intertongue with laminae of adjacent zooecial walls in an irregular zig-zag band so as to form a dark amalgamate-integrate outer wall. In tangential section the inner parts of the zooecial walls are well defined as distinct concentric bands. Concentric bands of adjacent zooecial walls are separated by a dark, amalgamate, and partly granulose outer wall. Acanthopores of variable diameter penetrate this amalgamate outer region of the zooecial walls and slightly inflect the outer part of the concentric inner walls. Central part of acanthopores is filled with calcite and surrounded by concentric laminae of acanthopore wall. Acanthopores and mesopores are generally located at the junctions of zooecial walls. Walls enclosing mesopores are similar in structure to zooecial walls and may be inflected by acanthopores. Mesopores are all shapes and sizes with no arrangement of the major axis of the opening in the direction of growth.

MEASUREMENTS OF HOLOTYPE IN MM.

Diameter of zoarial branch	3·32
No. of zooecial openings per 2 mm. . .	$3\frac{1}{2}$ to 4
Diameter of zooecial opening	min. 0·33 × 0·28 max. 0·44 × 0·42
No. of mesopores per zooecium	1 to 5
Diameter of mesopores	longitudinal axis 0·04 to 0·21 lateral axis 0·03 to 0·24
No. of acanthopores per zooecium . .	3 to 7
Diameter of acanthopores	0·015 to 0·027
Thickness of zooecial wall	0·07 to 0·14
Thickness of mesopore wall	0·04 to 0·08
Diameter of axial region	2·0
Axial ratio	0·6

REMARKS. The distinctive genus *Anaphragma* has so far been reported from only a few widely separated areas in the late Ordovician: " Maquoketa Group, Wilmington, Illinois " (Ulrich & Bassler 1904), and the " upper part of the Lyckholm limestone (F_1) at Kertel, and at Hohenholm on the island of Dago " (Bassler 1911 : 299).

The Portrane species has very little similarity to the type species, *A. mirabile* Ulrich & Bassler. *A. portranense* is similar to *A. mirabile* (as figured by Boardman 1960, pl. 3, fig. 3*c*) in the arrangement of the zooecial openings, mesopores and acanthopores. However, *A. portranense* has very slender cylindrical stems, larger zooecial openings and a slightly greater number of mesopores in comparison with *A. mirabile*. Both species have a wide range of sizes of mesopores, small acantho-

pores, and thick zooecial walls. In *A. portranense* the peripheral region is considerably narrower and the zooecial tubes bend more sharply than in *A. mirabile*, and, in addition, some of the smaller acanthopores are not restricted to the junctions of the zooecial walls as they are in *A. mirabile*.

The etched specimens PD.4425 (Pl. 6, fig. 5) and PD.4432 (Pl. 6, fig. 14) have general external features which suggest *Anaphragma*, but they are questionably assigned to the genus because their internal structures are not known.

Genus *CALOPORA* Hall

Calopora sp. A

(Pl. 3, figs. 1–4, 6, 8 ; Pl. 6, fig. 1)

MATERIAL. Includes PD.4394–96, 4422.

DESCRIPTION. A species of *Calopora* with round zooecial openings surrounded, but not completely isolated, by mesopores. Mesopores have closely spaced diaphragms. Less robust branches (Pl. 3, figs. 2, 3) have more slender zooecial walls and very few diaphragms in the peripheral region. Robust specimens (Pl. 3, figs. 6, 8) have numerous diaphragms in the peripheral region. Surface of colony has very distinct mounds (see left side of specimen Pl. 6, fig. 1) in which zooecial openings and mesopores have the usual average diameter.

REMARKS. This Portrane species can be compared with a number of typical species of *Calopora*. *C. elegantula* from the Rochester Formation, New York, has numerous angular mesopores which form a circlet around the circular zooecial openings. Diaphragms are widely spaced in the zooecial tubes and more closely spaced in the mesopores. In comparison with the Portrane species, *C. elegantula* has more numerous mesopores and diaphragms and the diaphragms are curved and sometimes incomplete. *C. incontroversa* (Ulrich) from " lower third of the Trenton shales at Minneapolis, St. Paul, and Preston, Minn." (Ulrich 1893 : 279) has more zooecial openings per 2 mm. and probably fewer mesopores per zooecium than the Portrane species. Both species have closely spaced diaphragms in the zooecial tubes in the peripheral and subperipheral regions separated by an intermediate region between them in which diaphragms are sparse or lacking. *C. dumalis* (Ulrich " common in *Phylloporina* bed of the Black River (Decorah) shales, and in the *Clitambonites* bed of the lowest Trenton at St. Paul and Cannon Falls, Minnesota," has similarities to *Calopora* sp. A in its slender cylindrical branches (1·5 to 2·0 mm. diameter) and in the shape and abundance and arrangement of mesopores. The two species are also alike in the spacing of the diaphragms, which are not crowded in the outer peripheral region. *C. dumalis* has a considerably greater number of zooecia per 2 mm. and zooecial tubes are oblique to the zoarial surface in young stages of growth. The two species are similar in the abundance and distinctness of mesopores.

Longitudinal sections of young growth stages of *Calopora* sp. A (Pl. 3, figs. 2, 3) have a sparsity of diaphragms in the zooecial tubes and closely spaced diaphragms in the mesopores as in *C. tolli* (Bassler 1911 : 333–334). However, the general

dimensions of the zoarial stem of *C. tolli* are considerably greater (6 to 8 mm.) in comparison to the Portrane species. Both species have a similar number of zooecial openings per 2 mm. and thin zooecial walls. *C. tolli* is reported " Rare in the Jewe limestone (D_1), Baron Toll's estate, Kuckers shale (C_2), Reval, and in the Kegel limestone (D_2), Kegel, Esthonia " (Bassler 1911 : 334). *C. gracilens* (Bassler) (1928 : 154–155) from the " Vaureal (4, 5), Battery and West Points," Anticosti Island, is similar to the Portrane species in the slender zoarial stems (2 mm. diameter) and the number of zooecial openings per 2 mm. (4 to 5 per 2 mm.). The Portrane species has distinct, elevated broad areas on its zoarial surface which are lacking in *C. gracilens*. In both species the mesopores appear crowded with diaphragms, but in the zooecial tubes the Portrane species has a generous scattering of diaphragms which are very sparse in *C. gracilens*. *C. subnodosa* (Ulrich) (1890 : 417, pl. 33, figs. 5–5*c*) from the " upper beds of the Cincinnati group, Blanchester, O., and numerous other localities " has considerably thicker zoarial stems, more abundant zooecial openings per 2 mm. and a wider peripheral region than the Portrane species. Though the two species are quite distinct, they are similar in the comparable abundance of mesopores around the zooecial openings, the arrangement of diaphragms in the mesopores, the thin zooecial walls, and the arrangement of diaphragms in the subperipheral region of the zooecial tube. However, diaphragms may be absent in the peripheral region of *C. subnodosa* and are present in the peripheral region of the Portrane species. *C. bassleri* (Hennig 1908 : 52–54, pl. 3, fig. 17; pl. 7, figs. 2, 10, text-figs. 62, 63) from "Lansa på, Fårö, Norderstrand vid Visby, Petesvik i Hablingo"

MEASUREMENTS in mm.

	PD.4394	PD.4395	PD.4422
Diameter of zoarial branch	1·8 incomplete	2·3	3·1 to 3·6
No. of zooecial openings per 2 mm. longitudinally	4 to 4½	3½ to 4	3 to 4
Diameter of zooecial openings	0·24×0·16 0·29×0·26	0·22×0·39	0·25×0·19 0·38×0·31
No. of mesopores per zooecium	6 to 7	Not determined	2 to 6
Diameter of mesopores	0·13×0·05 0·21×0·11	0·05 to 0·30 longitudinally	0·28×0·25 0·10×0·10
Thickness of zooecial wall	0·01 to 0·03	0·01 to 0·015	0·03 to 0·04
Thickness of mesopore wall	0·01 to 0·02	0·01 to 0·015	0·03 to 0·04

has certain similarities to the young growth stages of the Portrane species (Pl. 3, fig. 2) which closely resembles the longitudinal section illustrated by Hennig (1908, text-fig. 62). Hennig's specimen has more sparsely spaced diaphragms in the peripheral region and these are lacking in the Portrane specimen. *C. bassleri* has 6 zooecial openings per 2 mm. which is greater than that in the Portrane species and, in addition, *C. bassleri* appears to have slightly more mesopores around the zooecia openings.

Calopora sp. B

(Pl. 6, fig. 2)

MATERIAL. PD.4423.

DESCRIPTION. This form, represented by a single etched specimen, is characterized by slender branches with small zooecial openings that are almost isolated by a circlet of polygonal or occasionally round mesopores (Pl. 6, fig. 2). Maculae consisting of mesopores occur at intervals across the zoarial surface. The maculae, about 0·37 mm. × 0·30 mm., consist of flat areas of mesopores surrounded by large zooecial openings.

REMARKS. Without internal features it is difficult to make comparison with other species, but in the smaller size of the zooecial openings, greater abundance of mesopores, and the presence of maculae, this species differs from *Calopora* sp. A.

MEASUREMENTS in mm.

Diameter of zoarial branch	2·4 to 3·9
No. of zooecial openings per 2 mm. longitudinally	$6\frac{1}{2}$ to 7
Diameter of zooecial opening	0·22×0·27
	0·20×0·25
No. of mesopores per zooecium . . .	8 to 10
Diameter of mesopores	0·02×0·02 to 0·10×0·11
Thickness of zooecial wall	0·02 to 0·04
Diameter of mesopores	0·02 to 0·10

Genus ***DIANULITES*** Eichwald

Dianulites? sp.

(Pl. 2, figs. 1–8)

MATERIAL. Five thin sectioned fragments, PD.4385–89.

DESCRIPTION. Thin sections reveal colonies with very distinctive tangential sections. In shallow tangential sections (Pl. 2, figs. 1, 8) the subpolygonal zooecial openings are surrounded by small mesopores and wide zooecial walls ; deeper tangential sections display circular zooecial tubes and larger polygonal mesopores in concentric bands around the zooecia. The mesopore and zooecial walls are similar in structure and width and are finely granulate and amalgamate. Magnifications ×200 show that the inner part of a wall is lined with a narrow concentric band of granular calcite.

An oblique longitudinal section shows abundant diaphragms in the mesopores, and two or three diaphragms are visible in two of the zooecial tubes. The zooecial walls at magnifications ×200 have a distinct inner wall of longitudinal granular calcite which is indistinct at lower magnifications. Adjacent zooecial walls appear amalgamate and display a dense granular structure with a vague, slightly curved alignment of the calcite grains.

REMARKS. This form, so distinct in thin sections, appears very different from previously described species. Unfortunately, not all the features of a colony of this species are known because it has only been observed in a relatively small number of thin sections which do not display all features of the zooecial tubes.

It is difficult to place this species in any known genus because its distinctive features lack similarity to those of known genera. Initially a tangential section (Pl. 2, figs. 1, 8) with mesopores and round zooecial openings would suggest *Calopora*, but the granular wall structure is completely different from the laminate wall structure of *Calpora*. This difference is striking when, as in the Portrane Limestone material, the two different wall structures of *Dianulites?* and *Calopora* are viewed in the same thin section.

The species is questionably assigned to *Dianulites* because it has general similarities to some forms placed in the genus, for instance those described by Bassler (1911) from Estonia—however, none is closely similar to the Portrane species. The Estonian species have angular zooecial openings and thinner zooecial walls. Because little detailed morphology is known about *Dianulites*, redescription of the original type material of the genus is necessary in order to determine the taxonomic position of many European and North American species referred to it.

MEASUREMENTS in mm.

	PD.4385	PD.4386
Diameter of zooecial opening	min. 0·26×0·16	min. 0·22×0·27
	max. 0·54×0·42	min. 0·29×0·33
No. of zooecial openings per 2 mm.	approx. 3 to 3½	4 to 5
No. of mesopores around a zooecium	11 to 13	1 to 5
Dimensions of mesopores	0·04 square	0·02×0·13
	0·03×0·20 rectangle	0·17×0·11 rectangle
	0·10×0·42 rectangle	
	0·14 side of polygon	
Thickness of zooecial wall	0·05 to 0·08	0·10 to 0·13
Thickness of mesopore wall	0·02 to 0·05	0·04 to 0·08

The Portrane *Dianulites?* sp. is somewhat similar to the type species of *Phragmopora, P. multiporatum* Bassler (1911), from the Kuckers Limestone (C_2), near Jewe Estonia (Pl. 8, figs. 4, 6). Tangential sections of both species have round zooecial openings enclosed by regular polygonal mesopores which are concentrically arranged around the zooecial openings ; in addition, the wall structure appears similar. In longitudinal section, however, they are very different—*P. multiporatum* has hemiphragms in the zooecial tubes but they are lacking in *Dianulites?* sp.

Genus ***AMPLEXOPORA*** Ulrich

Amplexopora sp.

(Pl. 1, fig. 5 ; Pl. 4, figs. 8, 9 ; ?Pl. 7, fig. 12)

MATERIAL. PD.4393, 4406–7. Questionably assigned to the genus, PD.4444.

DESCRIPTION. Three fragments have delicate, possibly incrusting, laminate colonies with slender zooecial walls, numerous small but distinct acanthopores which slightly inflect the zooecial walls, and zooecial tubes and mesopores which have diaphragms. An occasional acanthopore appears on the inside of the mesopore wall. Acanthopores have distinctly thick walls with steeply inclined laminae. Zooecial walls are integrate but lack the distinct dark line which bounds the outer part of the zooecial wall in the genus *Batostoma*.

REMARKS. The few fragments of this species do not permit a detailed comparison with other species. However, they appear to belong to the species complex that includes the type species of *Amplexopora*. Tangential sections have a general resemblance to *A. septosa* (Boardman 1960, pl. 6, fig. 3*c*), in that both species have slender zooecial walls and inflecting acanthopores which are quite distinct. *A. septosa* is most probably a much more robust species. Its primary types are from the " Mount Hope shale member of the Fairview formation, Maysville group, of the upper Ordovician at Covington, Ky." (Boardman 1960 : 20). In specimens of *A. septosa* in which the zooecial walls are inflected there are about 4 to 5 acanthopores per zooecium and the Portrane species has 5 to 7. Zooecial openings of the two species are approximately of the same diameter. Another species belonging to the *A. cingulata-A. septosa* group is *A. affinis*. This species, described by Ulrich (1890 : 450–451, pl. 36, figs. 2–2*a*), is similar to the Portrane species in the distinctive acanthopores and thin zooecial walls.

An etched specimen (PD.4444—Pl. 7, fig. 12) with closely packed polygonal zooecial openings encircling a slender cylindrical stem is provisionally assigned to *Amplexopora*.

MEASUREMENTS of PD.4393 in mm.

Diameter of zooecial opening	0·24×0·16 to 0·21×0·16
Diameter of acanthopore	0·02 to 0·04
Diameter of mesopore	0·04×0·04 to 0·04×0·11
Acanthopores per zooecium	5 to 7
Thickness of zooecial wall	0·01

Genus *BYTHOPORA* Miller & Dyer

1878 *Bythopora* Miller & Dyer : 6.

Type species. *Bythopora dendrina* (James). Holotype, M.C.Z.2144 " middle part of the Cincinnati Group, at Cincinnati " (Miller & Dyer 1878 : 6).

Diagnosis. Very slender cylindrical branches with zooecial openings steeply inclined to periphery. Oval zooecial openings enclosed by amalgamate zooecial walls which are penetrated by three, four or five small acanthopores. Very shallow mesopores occurring in peripheral part of zooecial walls. In longitudinal sections zooecial walls composed of steeply inclined laminae curving convexly distally in median region between adjacent zooecial walls.

Bythopora? sp.

(Pl. 1, fig. 3)

Material. One thin section, PD.4392.

Remarks. An oblique longitudinal section shows limited characters of a tangential and longitudinal orientation through an exceptionally slender cylindrical stem provisionally assigned to *Bythopora*. In tangential view the circular zooecial openings are surrounded by small acanthopores (commonly 10 acanthopores per zooecium). The zooecial openings appear to rise obliquely to the periphery.

Measurements in mm.

Diameter of zoarial stem	1
Diameter of zooecial openings	0·13 to 0·16
Diameter of acanthopore	0·02 to 0·03

Order CRYPTOSTOMATA Vine

Genus *ENALLOPORA* d'Orbigny

1849 *Enallopora* d'Orbigny : 502.
1889 *Protocrisina* Ulrich : 317.
1890 *Protocrisina* Ulrich ; Ulrich : 369.

Type species : *Gorgonia perantiqua* Hall 1847 : 76.

Diagnosis. Colony with bifurcating branches. Celluliferous obverse surface with four rows of zooecia across a branch. Zooecial openings projecting distally above obverse surface. Two rows of zooecia on either side of median lamina. Finely granular, slightly curved reverse surface.

Enallopora perantiqua (Hall)

1847 *Gorgonia perantiqua* Hall : 76, pl. 26, figs. 5*a*, 5*b*.
1849 *Enallopora perantiqua* (Hall) d'Orbigny : 502.

Holotype. AMNH 665/1, figured by Hall 1847, pl. 26, figs. 5*a*, *b*, from " Trenton, Middleville, N.Y."

DESCRIPTION. Bifurcating colony, enclosed in black fissile shale, has four rows of circular zooecial openings on obverse surface which extends around 2/3 of the perimeter of the zoarial stem. The lateral rows of zooecia are directed outwards beyond the lateral margins of the zoarial stem ; diameter of lateral zooecial openings 0·11 to 0·14 mm. Two rows of median zooecia are separated by a median lamina ; zooecial openings are directed distally. Zooecial tubes extend as long cylindrical tubes originating near the reverse surface.

MEASUREMENTS in mm.

	AMNH 665/1
Width of zoarial branch	0·55 to 0·65
Angle of bifurcation of branches	12 to 35 degrees
Distance between bifurcation (varies in different parts of colony)	2·5 to 2·9 4·9 to 5·1
No. of zooecia per 2 mm. longitudinally in lateral ranges	4½
Thickness of zoarial branch	0·35
Diameter of zooecial opening	0·11 to 0·14

Enallopora sp. A

(Pl. 6, figs. 6, 7)

MATERIAL. Seven fragments, PD.4426–27, 4449–51, 4454–55.

DESCRIPTION. Very slender cylindrical bifurcating branches have no zooecia on the lower reverse surface which covers about 1/3 of the perimeter of branch. Four longitudinal rows of zooecia extend along the remaining 2/3 of the perimeter. Distally oblique zooecial openings at the zoarial surface extend in almost spiral arrangement diagonally and distally along the stem.

MEASUREMENTS in mm.

	PD.4426	PD.4427
Diameter of zoarial stem	0·5 to 0·6	0·5 to 0·6
Diameter of zooecial opening	0·20×0·15	0·20×0·15 0·17×0·12
No. of zooecia per 2 mm.	3 to 3½	3
Distance between successive zooecial openings	0·4 to 0·6	0·3 to 0·6

REMARKS. The Portrane species is externally similar to several species, including *Enallopora perantiqua* (Hall), *E. exigua* (Ulrich), *E. alliku* Männil, and *E. moe* Männil. The type material of *E. perantiqua* is very difficult to study owing to its preservation in a black fissile shale which crumbles readily, so that only part of the holotype (Hall 1847, pl. 26, figs. 5*a*, *b*) is now preserved. This species has a similar silhouette of lateral projecting zooecial openings, similar branch diameter, slightly more zooecial openings per 2 mm., and slightly smaller zooecial openings (0·11 to 0·14 mm.) in comparison with the Portrane species. *E. exigua* was noted by Ulrich (1890 : 405)

to be " rare at Wilmington, Ill., where it is associated with typical Cincinnati group fossils. It is more common and in a better state of preservation in Trenton group strata at Montreal, Canada, and Trenton Falls, N.Y."; compared with the Portrane species, this species has about the same branch diameter, more zooecial openings per 2 mm. (5 to $5\frac{1}{2}$ in 2 mm.) and smaller zooecial openings (0·09 mm.). *E. alliku* Männil from the Estonian D_1 to D_3, E?, has a slightly more slender zoarial stem, zooecial openings of about the same diameter, and a greater number of zooecial openings (4 to 5 per 2 mm.), in comparison with *Enallopora* sp. A. Both species have oblique zooecial openings ; those in the Portrane species appear to be the more oblique. The silhouette of both species from the reverse surface is similar. Compared with *Enallopora* sp. A, *E. moe* from the Estonian F_{1a} to F_{1c} has a considerably thicker zoarial stem and zooecial openings of about the same size, which are, however, more numerous per 2 mm. (4 to $4\frac{1}{2}$) and considerably more oblique.

Genus *MITOCLEMELLA* Bassler

1952 *Mitoclemella* Bassler : 381.

DIAGNOSIS. Zoarium ramose, very small (0·5 to 0·6 mm. diameter of branch). Tubular zooecia projecting strongly upward and outward and not constricted at the zooecial openings. Zoarial surface with faint transverse striae or wrinkles. (After Ulrich 1890 : 177).

TYPE SPECIES. *Mitoclema? mundulum* Ulrich (1890 : 177, text-fig. 4) ; " Top of Trenton Shales, at Cannon Falls, Minnesota."

REMARKS. When Ulrich (1890) described *Mitoclema? mundulum*, he was dubious that his species might not be a species of *Diploclema*. However, as he did not know the internal features of his species, he questionably assigned it to *Mitoclema*. Bassler (1952 : 381) erected *Mitoclemella* for a genus " Like *Mitoclema*, but apertures project upward in rapidly ascending spirals ". He did not re-describe the type species, so that only the external structures as given by Ulrich (1890) are known. The Portrane species, which provisionally appears to belong to this genus, is a collection of etched specimens and has not been determined in thin section.

***Mitoclemella*? sp. A**

(Pl. 5, fig. 3 ; Pl. 6, figs. 11, 12 ; Pl. 7, fig. 5)

MATERIAL. Nine etched specimens, PD.4419–21, 4437, 4446, 4452, 4458, 4464, and 4601.

DESCRIPTION. Branches large for the genus, cylindrical, with zooecial openings covering the entire surface. Zooecial tubes project obliquely upward and outward and show no constriction of the zooecial openings. Small pits, commonly single or paired, penetrate the zoarial surface in the longitudinal interspaces between succeeding zooecia. The zooecial openings are diagonally aligned along the zoarial stem, and on a weathered surface they are very irregular in outline.

MEASUREMENTS of PD.4420 in mm.

Diameter of zoarial stem	2·0
Diameter of zooecial opening	0·10 to 0·18
Diameter of pits	0·05

REMARKS. The Portrane species has considerably larger zoarial stems (2·0 mm.) than those of *M. mundulum* (Ulrich) (0·5 to 0·6 mm.). The diameter of the zooecial openings of the two species is, however, very similar. There is no reference in Ulrich's description to pits similar to those found in the Portrane species and in the present discussion these structures are regarded as only of specific criterion. Ulrich (1890 : 177) indicated that the zoarial surface between zooecia had faint transverse striae or wrinkles, but such features have not been observed in the Portrane material.

Genus ***PENNIRETEPORA*** d'Orbigny

1849 *Penniretepora* d'Orbigny : 501 (non d'Orbigny 1850 : 45).
1884 *Pinnatopora* Vine : 191.
1884 *Pinnatopora* Vine ; Shrubsole & Vine : 330.
Glauconome authors (non Goldfuss 1826).

DIAGNOSIS. " Deux rangées de cellules d'un seul côté d'un ensemble penniforms, composé d'une tige et de rameaux libres lateraux, non anastomosés." (d'Orbigny 1849 : 501).

TYPE SPECIES. *Retepora pluma* Phillips (1836 : 199, pl. 1, figs. 13–15).

REMARKS. *Penniretepora*, which ranges from the Ordovician to the Permian, includes many species that have had a complex nomenclatorial history, particularly those from the Ordovician and Silurian of Great Britain and western Europe which have been assigned to the genus *Glauconome* Goldfuss.

Penniretepora is used in the present study in preference to *Glauconome* and a brief digression on the nomenclatural history of *Glauconome* outlines the basis for this. The name *Glauconome*, originally used to define a pelecypod by Gray (1828), was inadvertently used by Goldfuss (1831) for a polyzoan. Thus in accordance with the International Rules of Zoological Nomenclature, *Glauconome* Goldfuss is a junior homonym and is to be rejected.

The nomenclature is further complicated because the generally accepted type species of *Glauconome* Goldfuss, *G. disticha* Goldfuss, was not one of the species in the original group of forms described by Goldfuss. Goldfuss's specimens of *G. disticha* were five in number—four have been re-assigned to the Tertiary to Recent genus, *Vincularia*, and the fifth is from the Silurian Wenlock Limestone, Dudley, England. It was this fifth specimen upon which the concept of *Glauconome* Goldfuss was developed, although it was embedded in rock so that many of the characters were not defined by Goldfuss.

Lonsdale (1839 : 677) re-defined *Glauconome* Goldfuss but based his re-description of *G. disticha* upon additional material from the Wenlock Limestone of Dudley, and not on Goldfuss' type material. However, it is hard to determine whether Lonsdale's

specimens were congeneric with Goldfuss's, a matter which Phillips (1841) and M'Coy (1854) apparently realized. *G. disticha* (Lonsdale 1839 : 677) was described as having " four rows of long quadrangular cells at one side." However, in most studies the forms assigned to Lower Paleozoic representatives of *Glauconome*, including Goldfuss's imperfectly known material, are stated to have two rows of zooecia along the obverse surface. Lonsdale's figures (1839, pl. 15, figs. 12, 12*a*, 12*b*) appear to represent forms which are more precisely described by M'Coy (1854) as having " two rows of cells on one face which is usually carinated between them; in some species a row of small cells on the keel." Some of the Portrane specimens, e.g., PD.4424, clearly display the features noted by M'Coy. Phillips (1841 : 21) likewise defined " *Glauconome* " as having two lines of zooecial openings along the branch, but noted that " there are signs of lateral rows in *G. disticha*." He was apparently referring to Lonsdale's material of *G. disticha* because he stated, " The single species of *Glauconome* of Goldfuss, to which this generic name had been preserved by Lonsdale." Some of this complicated history of " *Glauconome* " was discussed by Etheridge (1877).

Bassler (1952 : 384) erected the new name *Glauconomella* for " *Glauconome* authors, non Goldfuss, 1829, Petr. Germ., p. 100, pl. 36, figs. 5–8, based on unrecognizable *Vincularias* from the Tertiary of Germany ". He listed *Glauconome disticha* Goldfuss (1831 : 217, pl. 64, fig. 15*b*) as the type species of *Glauconomella*. *Glauconomella* may be a valid name as it is a new name for *Glauconome* (pars) Goldfuss, but, at present, because no revision has been undertaken of Goldfuss's type material, the detailed characters of *Glauconomella* and *G. disticha* (Goldfuss) are not known. Because d'Orbigny's description of the genus *Penniretepora* appears more precisely defined and because this genus appears to have characters closely similar to those attributed to *Glauconome* = *Glauconomella*, particularly with respect to the two rows of zooecial openings on the obverse surface, *Penniretepora* is used in the present study in preference to *Glauconomella*.

Penniretepora sp. A

(Pl. 6, fig. 3; Pl. 8, fig. 5)

MATERIAL. One etched specimen, PD.4424.

DESCRIPTION. Pinnate colony with the main stem slightly thicker than the lateral branches which are slanted obliquely to the main stem. Two rows of zooecia on sloping surfaces are separated by a noded median ridge. Lateral branches alternate on either side of the main stem and have similar structure to it. Reverse surface with faint longitudinal striae and knobbles. Zooecial openings consistently occur on the main stem at the junctions with the lateral stems.

MEASUREMENTS of PD.4424 in mm.

Diameter of main stem	0·35
Diameter of lateral branches	0·22
No. of zooecia per 2 mm. on main stem	8 to $8\frac{1}{2}$

No. of zooecia per 2 mm. on lateral stem	8
Diameter of zooecial opening on main stem	0·07×0·05 0·10×0·07
No. of zooecia on main stem between successive lateral branches	2
Distance between adjacent lateral branches	0·45
Distance between adjacent lateral branches on opposite sides of main stem	0·22
Nodes per 2 mm. on median ridge	8
Angle of divergence between side branches and main stem	60 to 70 degrees
Distance between centres of successive zooecial openings	0·20 to 0·25

REMARKS. The few Lower Paleozoic species of *Penniretepora* and *Glauconome* from England, Estonia, U.S.S.R., Scandinavia, and Australia, which are adequately described, appear to have no close similarity to the Portrane species. The Silurian species *P. lobata* Crockford (1941 : 110–111) from the Yass district, N.S.W., Australia, has a narrow main stem but the side branches and zooecial openings are considerably more widely spaced. Two species, *Glauconome plumula* Wiman and *G. strigosa* (Billings), discussed by Bassler (1911 : 159–162) from the Ordovician of Estonia, have no close similarity to the Portrane species ; *G. plumula*, for instance, apparently has four rows of zooecia on the obverse surface.

Penniretepora sp. B

MATERIAL. One etched specimen, PD.4447.

DESCRIPTION. Pinnate colony with two rows of zooecial openings on a slightly curved zoarial obverse surface. Reverse surface striated and striae also present between the zoarial branches and the zooecial openings. The faint median ridge has three rows of striae which are very distinct. Zooecial openings on the main stem are not in regular longitudinal lines because those which occur at junctions of main stems and lateral branches are displaced on to the lateral branches.

MEASUREMENTS of PD.4447 in mm.

Diameter of main zoarial stem	0·5
Diameter of lateral zoarial stems	0·2 to 0·3
No. of zooecia per 2 mm. longitudinally on main stem	7
No. of zooecia on main stem between lateral branches	1
Diameter of zooecial openings	0·10×0·12
Distance between centres of adjacent lateral branches	0·55 to 0·65

REMARKS. This species differs from *Penniretepora* sp. A in having larger zooecial openings on a nearly flat obverse surface, a thicker main stem, striae on the obverse surface, and a very different grouping of zooecial openings between the lateral branches.

Genus *PSEUDOHORNERA* Roemer

1876 *Pseudohornera* Roemer : Explanation of pl. 12.
1890 *Drymotrypa* Ulrich : 399.

DIAGNOSIS. Colonies dichotomously branching. Zooecia in several ranges. Zooecial openings angular at the zoarial surface, becoming oval a short distance below the zoarial surface. Reverse surface longitudinally striated.

TYPE SPECIES. *Retepora diffusa* Hall (1852 : 160, pl. 40*c*, figs. 1*a–f*). "Niagaran (Rochester) of New York."

Pseudohornera? sp. A

(Pl. 6, fig. 8 ; Pl. 7, fig. 6)

MATERIAL Three etched specimens, PD.4428, PD.4438, PD.4466.

DESCRIPTION. Fragments may be parts of closely bifurcating branches or broken fenestrules of anastomosing colonies. Colony has apparently smooth reverse surface and an obverse surface with three to four rows of oval zooecial openings ; long axis of zooecial opening is in direction of growth of branch. Zooecia alternate but are not in longitudinal ranges.

MEASUREMENTS in mm.

	PD.4428	PD.4438
Width of zoarial branch	1	0·8
Diameter of zooecial opening	0·30–0·32 ×0·16–0·17	0·30×0·12
No. of zooecial openings per 2 mm. longitudinally	4	$4\frac{1}{2}$

REMARKS. These fragments can only be identified as to genus with any degree of certainty. Among the species assigned to *Pseudohornera*, the Portrane species has little similarity to *P. bifida excedens* Männil (1958) from C_3 to E of the Ordovician of Estonia, but has some general similarities in diameter of zoarial branch and size of zooecial opening to *P. striata* Männil (1958) from C_3 of the Ordovician of Estonia The latter species has seven to eight rows of zooecial openings across a zoarial branch, $5\frac{1}{2}$ to 6 zooecial openings per 2 mm., a striated non-celluliferous reverse surface, and zooecial openings which are generally smaller. *P. dichtoma* (Ulrich) (1890 : 399–400) from the " Trenton ", Montreal, Canada, is similar to the Portrane species in having four ranges of zooecial openings on a zoarial branch, but Ulrich's species has more slender zoarial branches, smaller zooecial openings, and more numerous zooecial openings per 2 mm.

Pseudohornera? sp. B

(Pl. 7, fig. 4 ; ?Pl. 5, figs. 1, 2, 6)

MATERIAL. One etched specimen, PD.4436. Questionably assigned to this taxon, PD.4408–09.

DESCRIPTION. The colony has a smooth reverse surface, and a highly curved obverse surface with weathered oblique polygonal zooecial openings. These openings could be oval on an unweathered surface. The bifurcating fragmentary branches may be part of a reticulate colony but they do not permit determination of this character.

MEASUREMENTS of PD.4436 in mm.

Diameter of zoarial branch	0·7
Diameter of zooecial opening	0·28–0·20 ×0·20
No. of zooecial openings per 2 mm. longitudinally . . .	7

REMARKS. This fragment differs from *Pseudohornera?* sp. A primarily in the greater number of zooecial openings per 2 mm. This feature could vary in different parts of a colony, but at present it seems that the difference in the fragments should be noted so that when more material is available later the limits of the different species can be more clearly defined.

Thin sections (PD.4408 and 4409—Pl. 5, figs. 1, 2, 6) of a species which appears to have features suggesting *Pseudohornera* are questionably assigned to this taxon.

Genus ***PTILODICTYA*** Lonsdale

1839 *Ptilodictya* Lonsdale : 676.
1960 *Ptilodictya* Lonsdale ; Ross : 1064.

DIAGNOSIS. Bifoliate colonies with ribbon-shaped or explanate forms of growth ; very distinct median set of ranges with a set of lateral ranges on either side. Mesopores and acanthopores lacking. Zooecial walls with escharoporid wall structure. Hemisepta present. Mesotheca simple and lacking median tubuli.

TYPE SPECIES. *Flustra lanceolata* Goldfuss (1829 : 104, pl. 37, figs. 2*a*–*d*).

Ptilodictya sp. A

(Pl. 7, fig. 1)

MATERIAL. Etched fragments of zoarial stems, PD.4433, 4461 and 4463? (deeply etched).

DESCRIPTION. Slender zoarial stems display no bifurcations. Almost square zooecial openings occur in the median ranges and rectangular zooecial openings in the lateral ranges.

MEASUREMENTS of PD.4433 in mm.

Zoarial width	2 incomplete
No. of zooecial openings per 2 mm. longitudinally in median ranges	8
No. of zooecial openings per 2 mm. longitudinally in lateral ranges	8

No. of median ranges	6
No. of lateral ranges on either side of median ranges . .	4
Diameter of zooecial opening	Median range
	0·25×0·20
	0·21×0·20
	Lateral range
	0·35×0·17
	0·40×0·18

REMARKS. *Ptilodictya* sp. A is similar to such delicate species as *P. ensiformis* (Hall) (Ross 1960 : 1067–1069) which ranges from the English Head Formation through the Jupiter Formation (Cincinnatian to Niagaran), Anticosti Island, and *Dicranopora emacerata* (Nicholson) from the "Cincinnati Group, near Cincinnati, Ohio". In comparison with *Ptilodictya* sp. A, *P. ensiformis* has a narrower zoarial stem, fewer ranges on a stem, and smaller, more rectangular zooecial openings.

Ptilodictya sp. B

(Pl. 7, fig. 3 ; ?Pl. 4, figs. 1–7)

MATERIAL. Two etched specimens, PD.4435, 4462. Questionably assigned to this genus, PD.4401–05.

DESCRIPTION. Wide zoarial stems with rectangular zooecial openings in both median and lateral ranges.

MEASUREMENTS of PD.4435 in mm.

Zoarial branch width	6 to 7
No. of median ranges	7 to 8
No. of lateral ranges	4 to 5
No. of zooecial openings per 2 mm. longitudinally in median ranges	5
No. of zooecial openings per 2 mm. longitudinally in lateral ranges	4
Diameter of zooecial opening in median and lateral ranges .	0·35×0·20
	0·37×0·17

REMARKS. This species is represented by a considerably wider zoarial stem than *Ptilodictya* sp. A. It is a typical species of the genus *Ptilodictya*, belonging to the group that includes *P. lanceolata* (Goldfuss) from the Upper Llandovery to Lower Ludlow of Gotland and the Wenlock of England, and *P. canadensis* Billings from the English Head Formation to Jupiter Formation (Cincinnatian to Niagaran), Anticosti Island. In comparison with these two species, *Ptilodictya* sp. B, though 6 to 7 mm. in width, has fewer longitudinal ranges across the branch and longer zooecial openings.

A number of incomplete zoarial fragments which were observed only in thin section (PD.4401–05—Pl. 4, figs. 1–7) are questionably placed in this species because not all features of the colonies are determinable. PD.4402 (Pl. 4, fig. 2) has 5 to 6

zooecial openings per 2 mm. and the zooecial openings measure 0·22 to 0·32 × 0·10 to 0·12 mm. in the median ranges. These measurements suggest that the fragment may be assignable to *Ptilodictya* sp. B which has fewer zooecial openings per 2 mm. than *Ptilodictya* sp. A.

Ptilodictya sp. C

MATERIAL. One etched specimen, PD.4456.

REMARKS. This small fragment, which is part of a wide zoarial branch, appears to have some similarity to *Ptilodictya* sp. B, from which it differs in having thinner zooecial walls, more elongate and narrower zooecial openings, fewer median ranges, and a greater number of lateral ranges.

MEASUREMENTS in mm.

Zoarial branch width	4·2 incomplete
No. of median ranges	4 to 5
No. of lateral ranges	9 to 10
No. of zooecial tubes per 2 mm. longitudinally in median ranges	$5\frac{1}{2}$
No. of zooecial tubes per 2 mm. longitudinally in lateral ranges	4 to $4\frac{1}{2}$
Diameter of zooecial opening in median range . .	0·32×0·07 0·35×0·10
Diameter of zooecial openings in lateral ranges . .	0·37×0·10 0·42×0·12

Genus ***PACHYDICTYA*** Ulrich

Pachydictya sp. A

(Pl. 7, fig. 10; ?Pl. 5, figs. 8, 9)

MATERIAL. PD.4415–16, 4442. Questionably assigned to this taxon, PD.4413–14.

REMARKS. The slender zoarial stem lacks any kind of lateral margin. This form differs from *Pachydictya* sp. B in having a more delicate colony, narrower zoarial stem, and larger zooecial openings.

MEASUREMENTS of PD.4442 in mm.

Width of zoarial branch	2·6
No. of zooecial openings per 2 mm. longitudinally . .	4
Diameter of zooecial opening	0·30 to 0·35 ×0·15 to 0·17

Specimen PD.4416 appears to belong to this species because it has a zoarial branch width of 1·32 mm. incomplete; $5\frac{1}{2}$ zooecial openings per 2 mm. longitudinally; diameter of zooecial opening 0·18 to 0·21 × 0·10 to 0·13 mm.; no apparent lateral

margin; and zooecial wall thickness of 0·026 to 0·042 mm. The thick zooecial walls have a distinct peristome around the zooecial openings and wide areas between the zooecial openings. Another specimen, PD.4415, appears also to belong to this species. Its zoarial stem depth is 1·43 mm.; the diameter of the zooecial opening is 0·21 × 0·13, and the thickness of the peristomal wall is 0·026 to 0·042 mm. Two thin sections (PD.4413–14—Pl. 5, figs. 8, 9), although oriented obliquely, appear to have delicate zoarial features comparable to *Pachydictya* sp. A.

Pachydictya sp. B

(Pl. 7, fig. 11)

MATERIAL. PD.4443 and 4457.

REMARKS. The two fragments of robust zoarial stems have wide non-celluliferous margins, round zooecial openings in longitudinal ranges, and papillose walls suggesting acanthopores that encircle the zooecial openings. Interspaces are not apparent in these etched specimens, but they may be covered by interstitial material.

MEASUREMENTS of PD.4443 in mm.

Width of zoarial branch	4·5
No. of zooecial openings per 2 mm. longitudinally . .	5
Diameter of zooecial tubes	0·25 to 0·32 ×0·17 to 0·25
Width of lateral margin	0·5 to 0·6

Genus ***STICTOPORA*** Hall

1847 *Stictopora* Hall: 73.
1849 *Sulcopora* d'Orbigny: 499.
1882 *Rhinidictya* Ulrich: 152.
1890 *Rhinidictya* Ulrich; Ulrich: 388, 492.
1921 *Hemidictya* Coryell: 303.
1960 *Stictopora* Hall; Phillips: 7.
1961 *Stictopora* Hall; Ross: 336.

DIAGNOSIS. Bifoliate branching colonies with zooecial openings in longitudinal ranges. Acanthopores encircling zooecial openings. Mesotheca penetrated by numerous median tubuli. Hemisepta and diaphragms may be present.

TYPE SPECIES. *Stictopora fenestrata* Hall (1847, pl. 4, figs. 4*a*–*d*).

REMARKS. *Stictopora* Hall is used in the present discussion in preference to its junior synonym *Rhinidictya* Ulrich which was extensively used in the past few decades by Ulrich and Bassler. Ulrich (1890: 492) stated that *Rhinidictya* was *Stictopora* Hall and examination of the type species of both genera substantiates Ulrich's statement.

Stictopora sp.

(Pl. 5, figs. 4, 10 ; Pl. 7, fig. 2 ; ?Pl. 5, fig. 7)

MATERIAL. PD.4434, 4410. Questionably assigned to the genus, PD.4412, 4417, 4459.

REMARKS. The few fragments of *Stictopora* which are present in the Portrane Limestone can only be identified as to genus. From the few features and measurements that can be determined, this form has wider zoarial branches and fewer zooecial openings per 2 mm. than the type species, *S. fenestrata*.

MEASUREMENTS of PD.4434 in mm.

Width of zoarial branch	2·7 to 3·0 incomplete
No. of zooecia per 2 mm. longitudinally . .	4 to $4\frac{1}{2}$
Diameter of zooecial openings	0·25 to 0·17 × 0·08 to 0·10
No. of ranges per 2 mm. laterally . . .	11

Several fragments of *Stictopora* are grouped in this discussion and it is not possible to determine from the fragmentary material if they are conspecific. PD.4410 (Pl. 5, figs. 4, 10) has $6\frac{1}{2}$ to 7 zooecial openings per 2 mm., zoarial stem width of 1·76 mm. incomplete, at least 10 ranges across the branch, and zooecial openings 0·16 to 0·18 × 0·08 to 0·10. This fragment has smaller zooecial openings and slightly more numerous zooecial openings per 2 mm. than PD.4434. PD.4412 (Pl. 5, fig. 7) is a very distinctive transverse section with median tubuli and acanthopores in the peripheral region ; zoarial width is 0·77 mm. and zoarial depth is 0·66 mm. An unfigured specimen, PD.4417, longitudinal section, has a narrow peripheral region (0·04 mm.), thin zooecial walls, zoarial depth of about 0·55 mm., and about 5 to 6 zooecial openings per 2 mm.

Genus ***ICHTHYORACHIS*** M'Coy

1844 *Ichthyorachis* M'Coy : 205.

TYPE SPECIES. *Ichthyorachis newenhami* M'Coy (1844 : 205) by monotypy.

DIAGNOSIS. " Gen. Ch.—Coral plumose, composed of a straight, central stem or midrib, having on each side a row of short, simple branches or pinnae, all in the same plane ; obverse both of the midrib and lateral branches rounded, without keel, and each bearing several rows of small, prominent, oval pores, arranged in quincunx ; reverse rounded, smooth, or finely striated." (M'Coy, 1844, p. 205).

REMARKS. M'Coy further stated, " The present genus stands nearly in the same relations to *Glauconome*, Lons., as *Polypora*, M'Coy, does to *Fenestella*, Miller. *Fenestella* and *Glauconome* are carinate on the obverse, and bear two rows of large, prominent pores, while *Polypora* and *Ichthyorachis* are rounded on the obverse, and bear several rows of small pores arranged in quincunx. . . ."

Cf. *Ichthyorachis* sp.

(Pl. 6, fig. 13)

MATERIAL. PD.4431.

DESCRIPTION. Pinnate zoarium has thick main stem and thinner lateral branches. Both the main and lateral branches appear to have the same number of zooecial ranges on their obverse surfaces; the zooecial openings are aligned in one median longitudinal range, two lateral longitudinal ranges (one on each side of the median range) and two irregular lateral rows which are partly discontinuous owing to junctions of lateral branches with the main stem. The zooecial openings are normal to the zoarial surface in the median and two lateral ranges, but oblique in the irregular lateral ranges. The reverse surface is smooth, that of the main branch slightly keeled.

MEASUREMENTS in mm.

Diameter of main zoarial branch	1·8
Diameter of lateral zoarial stems	0·9 to 1·0
No. of zooecial openings per 2 mm. on main stem . . .	4 to 5
Diameter of zooecial openings	0·30 × 0·15
	0·32 × 0·17

REMARKS. This species does not appear to have close similarities to previously described polyzoans. Initially it appears to be similar to *Pteropora,* but Männil (1958) has shown that this genus is bifoliate whereas the Portrane species is bipartite. *Ichthyorachis* M'Coy appears to be the only genus with which the Portrane specimen can be compared. Nevertheless, *Ichthyorachis,* which to date has been found in Devonian to Permian rocks, is still distinctly different from the Portrane specimen. The general similarity between M'Coy's material and the Portrane specimen lies in the pinnate form of both colonies and the number of zooecial openings across the branch. Both forms have five longitudinal ranges of zooecia on the main stem. However, *Ichthyorachis* does not have the distinct longitudinal ridges which separate the five longitudinal ranges of zooecial openings on the Portrane specimen. The two forms may belong to the same evolutionary lineage or may represent independent parallel evolution of features found in both forms. Unfortunately the internal characters of neither form are known. It seems advisable at this time to compare the Portrane species with *Ichthyorachis.* If the Portrane species belongs to this genus it means that the range of the genus extends back to at least the late Ordovician.

Genus ***HELOPORA*** Hall

Helopora? sp.

(Pl. 3, fig. 5; Pl. 6, fig. 4; Pl. 7, fig. 7)

MATERIAL. PD.4418, 4439, 4400.

REMARKS. The zoarium is slender, bifurcating. The zooecial openings are oblique, directed distally, occur round the zoarial branch, and have peristomes apparently with a circlet of fine pin-heads which may be acanthopore-like structures.

The zooecia alternate in adjacent longitudinal rows, but because the zooecial openings abut in an interlocking pattern the ranges are not clearly defined. In specimen PD.4439 the number of zooecia per 2 mm. is $3\frac{1}{2}$; diameter of zoarial branch is 0·8 mm.; and the diameter of the zooecial openings is 0·12 × 0·10. In external appearance the Portrane form has general features which suggest affinities to *Helopora* and the figured specimen is assigned to this genus with doubt. The transverse section of a very slender polyzoan (PD.4418—Pl. 6, fig. 4) looks much like the section that was figured as *Helopora lindstromi* from "Upper Silurian, Gotland" by Ulrich (1890, text-fig. 18*g*). Both are similar in the arrangement of the zooecial walls, which form a radiating spoke-like pattern, and in the considerably thickened zooecial walls in the peripheral region. The Portrane specimens do not appear similar in external appearance to species which were assigned to *Helopora* from Anticosti Island by Bassler (1928).

Genus ***NEMATOPORA*** Ulrich

Nematopora? sp.

(Pl. 7, fig. 8)

MATERIAL. PD.4440, 4465.

REMARKS. Specimen PD.4440 (Pl. 7, fig. 8) is a very slender colony (0·9 mm. diameter) with very narrow zooecial openings (0·22 to 0·27 × 0·03 to 0·05 mm. extending all around the stem. This etched specimen and PD.4465 appear to be similar to various forms placed in *Nematopora*, e.g., species of *Nematopora* illustrated by Ulrich (1890, pl. 29, text-figs. 7*a*, 10*a*). Because the internal structures of the two Portrane specimens are not known, they are doubtfully assigned to the genus. *Orthopora* Hall has longitudinal rows of slit-like zooecial openings separated by nodose ridges which are not present in the Portrane specimens.

Genus "***PHYLLOPORINA***"

"***Phylloporina***" sp.

MATERIAL. PD.4448.

DESCRIPTION. Irregular anastomosing branches with long narrow fenestrules and an occasional transverse dissepiment. Obverse surface has two rows of round zooecial openings on steeply sloping faces which meet in a poorly defined ridge. The ridge may have nodes but it is difficult to determine in this etched specimen. The apparently smooth reverse surface is possibly faintly striate. $7\frac{1}{2}$ to 8 zooecial openings per 2 mm., and zoarial stem width is 0·2 to 0·3 mm.

REMARKS. The irregular meshwork with occasional dissepiments and zooecial openings on steeply sloping faces suggests *Reteporina* d'Orbigny (Miller 1962: 545–546), but this genus lacks the ridge between the lateral sloping faces which is present in the Portrane specimen. Until more of the phylloporinid genera are more precisely defined, the Portrane specimen is assigned to "*Phylloporina*".

PHYLLOPORINID

(Pl. 5, fig. 7; Pl. 6, fig. 10)

MATERIAL. PD.4412, PD.4430.

DESCRIPTION. Reticulate or fenestrate zoarium with rectangular arrangement of branches. Zooecia are present on branches and cross-bars. Generally three to four ranges of round zooecial openings across the obverse side of a branch. The reverse surface is non-celluliferous and very faintly striate. These striae may be zooecial walls showing through the translucent etched surface.

MEASUREMENTS in mm.

Zoarial branch width	0·5 to 0·6
No. of zooecia per 2 mm.	10
Diameter of zooecial opening	0·15 to 0·18 ×0·12 to 0·15
Length of cross-bar	0·2 to 0·5
Width of cross-bar	0·4 to 0·6

REMARKS. This form has general similarities to such phylloporinids as *Sardesonina, Trepostomina,* and *Subretepora.* Unfortunatley this species has only been found in thin sections and all characters are not available for specific or generic determination.

Order CYCLOSTOMATA Busk

Genus ***HEDERELLA*** Hall

Hederella (Hederella) sp.

MATERIAL. PD.4453.

DESCRIPTION. The unfigured specimen PD.4453 is a small fragment of a hederelloid with the long zooecial tubes budding in various directions and different planes. Diameter of zooecial tubes is 0·6 mm. and distance between successive buds is 2·3 to 2·5 mm.

Genus ***CLONOPORA*** Hall

Clonopora? sp.

(Pl. 7, fig. 9)

MATERIAL. PD.4441.

DESCRIPTION. Specimen, PD.4441 (Pl. 7, fig. 9) consists of isolated zooecial tubes that open all around the colony. The zooecial openings do not appear to be constricted. It is not possible to determine from the fragment if the zooecial tubes are arranged in a spiral. It most closely resembles *Clonopora,* which has previously been identified only from the Lower Devonian. Diameter of zooecial opening is 0·31 × 0·37 mm. and the length of the zooecial tube before curvature is 1·0 mm.

Family DIASTOPORIDAE Gregory

Genus *DISCOSPARSA* d'Orbigny

Discosparsa? sp.

(Pl. 8, figs. 1–3, 7)

MATERIAL. Two etched specimens, PD.4468, 4469.

DESCRIPTION. Small cupuliform zoaria with smooth outer wall enclosing cup-like colony. The colony has a broad calyx filled with zooecial tubes closely packed together in regular radial and circular patterns. Direct zooecial tubes in the outer two circlets at the perimeter of the colony are round to oval in outline and smaller than the slightly oblique zooecial tubes that comprise the remainder of the colony. The zooecial tubes are more irregular in outline in the axial region and approach a polygonal outline.

MEASUREMENTS in mm.

	PD.4468	PD.4469
Diameter of calyx	10–12 incomplete	8
Height of colony	8	5–6
Size of zooecial tube in cross-section	0·5 to 0·7 in axial region, 0·3 at perimeter	0·4 to 0·5 in axial region, 0·3 at perimeter

REMARKS. This puzzling Portrane species belongs to the Diastoporidae. Among the Palaeozoic genera which have so far been described, it appears similar to *Berenicea*, but its closely packed zooecial tubes in regular radial arrangement in a cup-like colony differentiate it from *Berenicea*, which includes unilamellar subcircular sheets of loosely aggregated zooecial tubes. The Portrane form most closely approaches *Discosparsa*, described by d'Orbigny from the Cretaceous of France. It has the same form of colony and the same arrangement of zooecial tubes as such species as *D. laminosa* d'Orbigny and *D. cupola* d'Orbigny (cf. Pl. 8, figs. 1–3, 7 with d'Orbigny, 1850–1851, pl. 757, figs. 12–14; pl. 758, figs. 2, 4). D'Orbigny's species appear to be smaller in zoarial size than the Portrane species.

Polyzoa or *Algae*

(Pl. 6, fig. 9; Pl. 7, fig. 13)

MATERIAL. PD.4429 and 4445.

REMARKS. These two specimens of doubtful systematic position are also included in the Portrane fauna.

III. ACKNOWLEDGMENTS

I am grateful to Dr. A. D. Wright, Queen's University, Belfast, for lending me this material for examination and for his kind assistance with numerous enquiries about the Portrane fauna; and to Professor N. D. Newell, American Museum of

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PLATE 1

Anaphragma portranense sp. nov. p. 111

FIG. 1. Tangential section showing amalgamate part of zooecial walls penetrated by small acanthopores. P.D. 4390. ×50.

FIG. 2. Portion of longitudinal section showing general aspect of zooecial tubes, mesopores, and crenulate zooecial walls. P.D. 4390. ×50.

FIG. 4. Oblique longitudinal section showing general aspect of zooecial tubes, mesopores, and crenulate zooecial walls. PD. 4390. ×20.

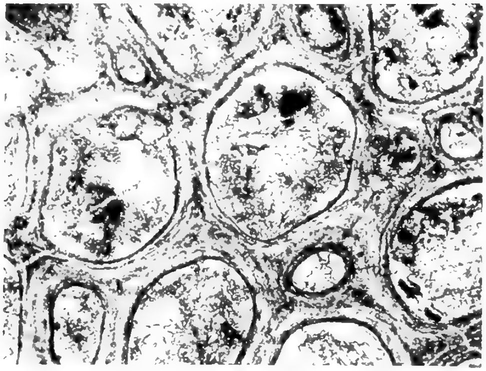
FIG. 6. Portion of oblique longitudinal section showing overgrowth on zoarial stem. PD. 4391. ×20.

Bythopora? sp. p. 118

FIG. 3. Oblique longitudinal section with acanthopores in peripheral region. PD. 4392. ×20.

Amplexopora sp. p. 117

FIG. 5. Oblique longitudinal section showing diaphragms in zooecial tubes and mesopores and acanthopores penetrating zooecial walls. PD. 4393. ×20.



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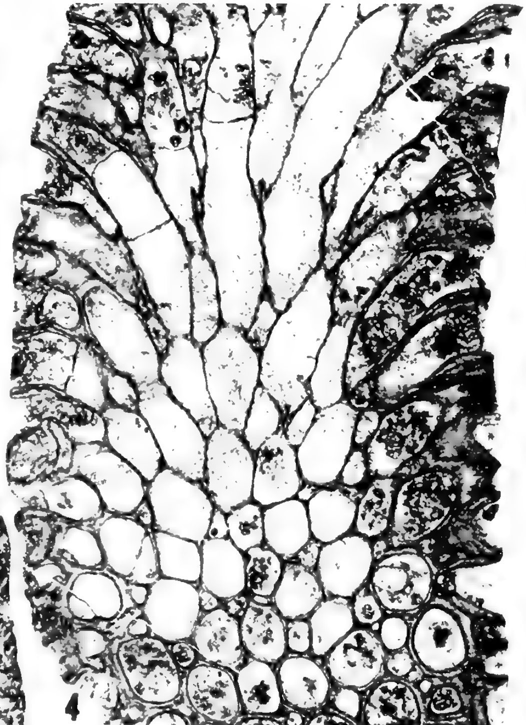

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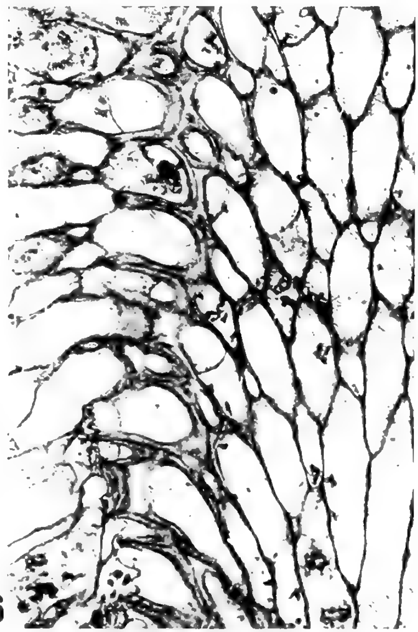

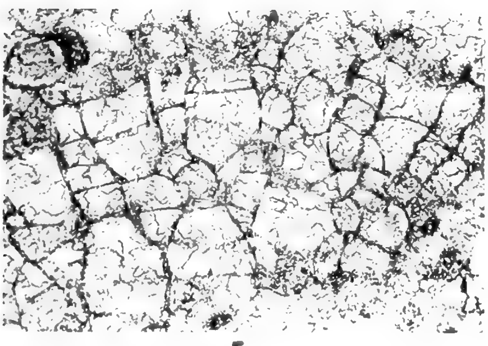

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PLATE 2

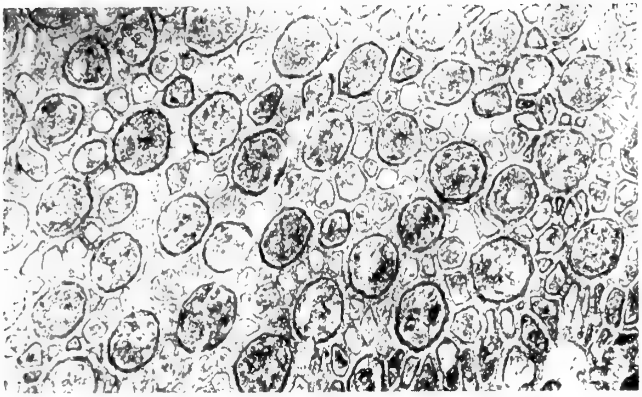
***Dianulites*? sp.** p. 115

FIGS. 1, 8. Tangential sections showing circular zooecial openings almost completely enclosed by concentric band of polygonal mesopores. PD. 4385. ×20 and ×50, respectively.

FIGS. 2, 5. Shallow tangential sections showing dense granular walls enclosing subpolygonal mesopores and zooecial openings. PD. 4386. ×50 and ×20, respectively.

FIGS. 3, 4. Part of oblique longitudinal section showing dense granular walls and diaphragms in the mesopores. PD. 4387. ×50 and ×20, respectively.

FIGS. 6, 7. Shallow tangential section showing zooecia and mesopores without distinctive symmetric pattern such as in Figs. 1 and 8. PD. 4388 and PD. 4389, respectively. ×50 and ×20, respectively.



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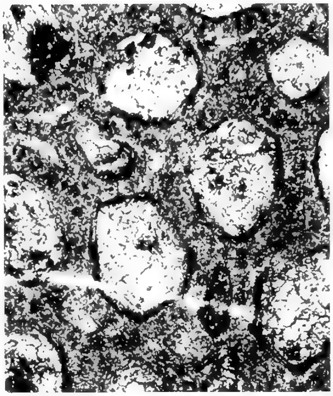

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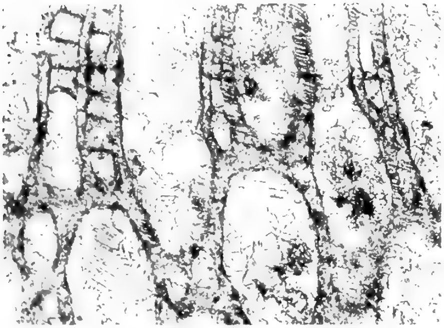

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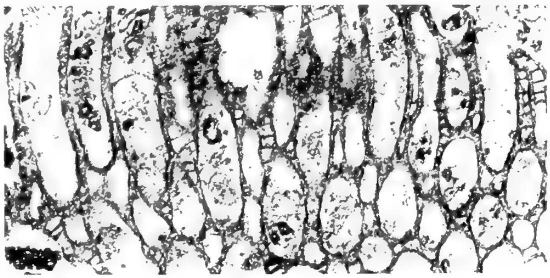

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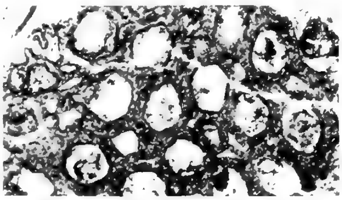

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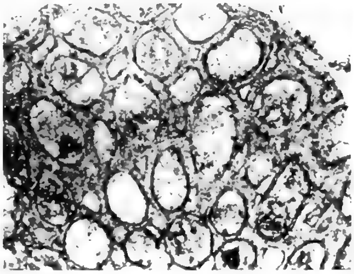

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PLATE 3

Calopora sp. A p. 113

FIG. 1. Tangential section showing well defined concentric bands of inner parts of zooecial walls separated by clear amalgamate outer parts of zooecial walls; narrower inner parts of mesopore walls separated by narrow amalgamate outer part. PD. 4394. ×50.

FIGS. 2, 3. Parts of longitudinal section showing slender zooecial walls, sparse diaphragms in zooecial tubes, and closely spaced diaphragms in mesopores. PD. 4395. ×20 and ×50, respectively.

FIG. 4. Oblique transverse section showing general aspect of zooecial tubes in axial and peripheral regions. PD. 4396. ×20.

FIG. 6. Oblique tangential section showing general arrangement of zooecial openings and diaphragms in zooecial tubes and mesopores. PD. 4394. ×20.

FIG. 8. Part of longitudinal section in peripheral region showing overlapping diaphragms in zooecial tubes and flat diaphragms in mesopores. PD. 4394. ×50.

Helopora? sp. p. 130

FIG. 5. Transverse section showing zooecial walls converging in axial region and subtriangular shape of zooecial tubes. PD. 4400. ×50.

Calopora? sp.

FIG. 7. Longitudinal section in peripheral region showing numerous diaphragms in zooecial tubes. PD. 4399. ×20.

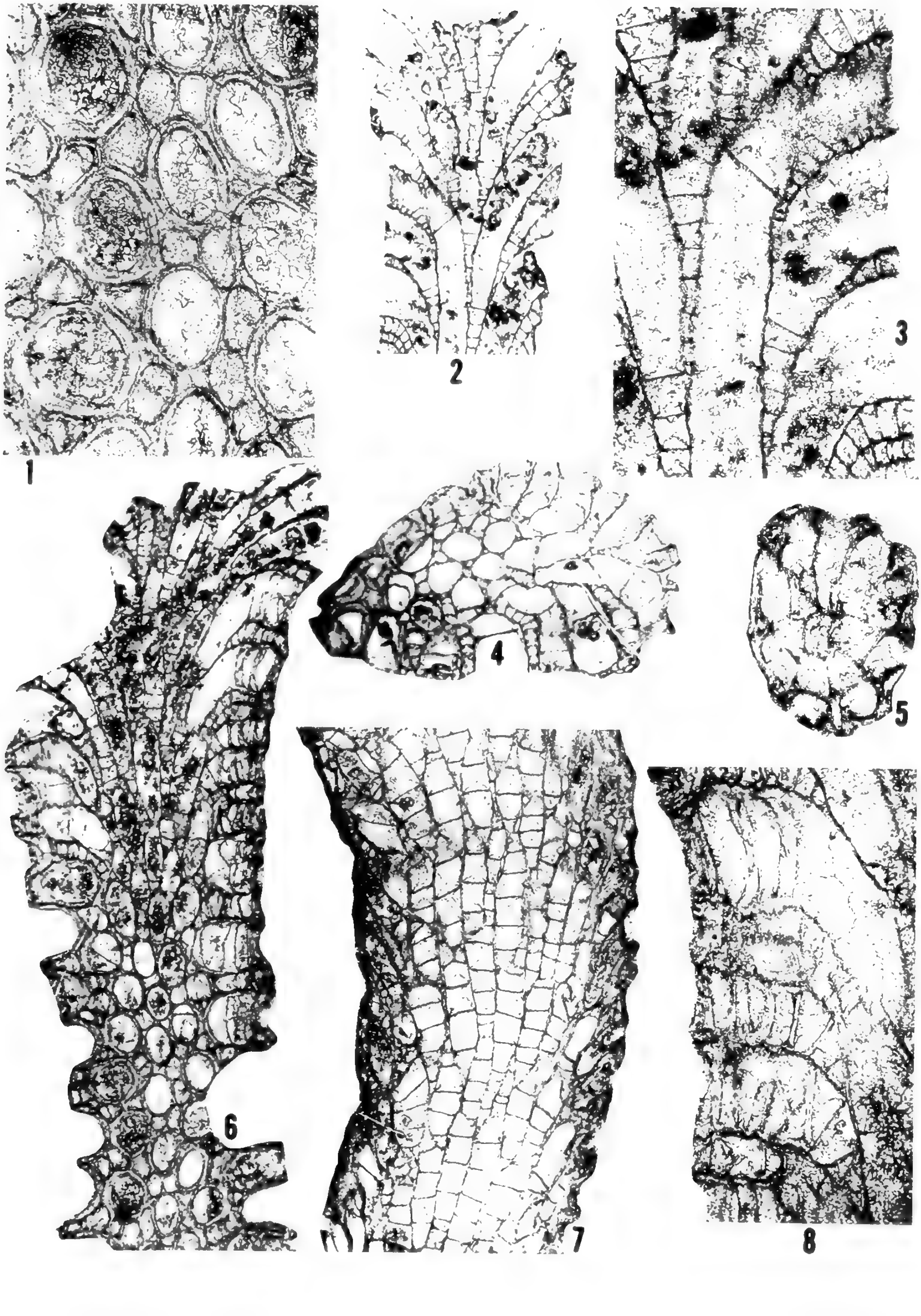
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PLATE 4

Ptilodictya sp. B? p. 126

FIGS. 1, 4. Tangential section. PD. 4401. ×20 and ×50, respectively.
FIG. 2. Tangential section. PD. 4402. ×20.
FIG. 3. Longitudinal section. PD. 4403. ×50.
FIGS. 5, 6. Oblique transverse sections. PD. 4404. ×50.
FIG. 7. Oblique longitudinal section. PD. 4405. ×50.

Amplexopora sp. p. 117

FIGS. 8, 9. Tangential sections showing well defined acanthopores penetrating integrate zooecial walls; small and numerous mesopores. PD. 4406 and PD. 4407, respectively, ×50.

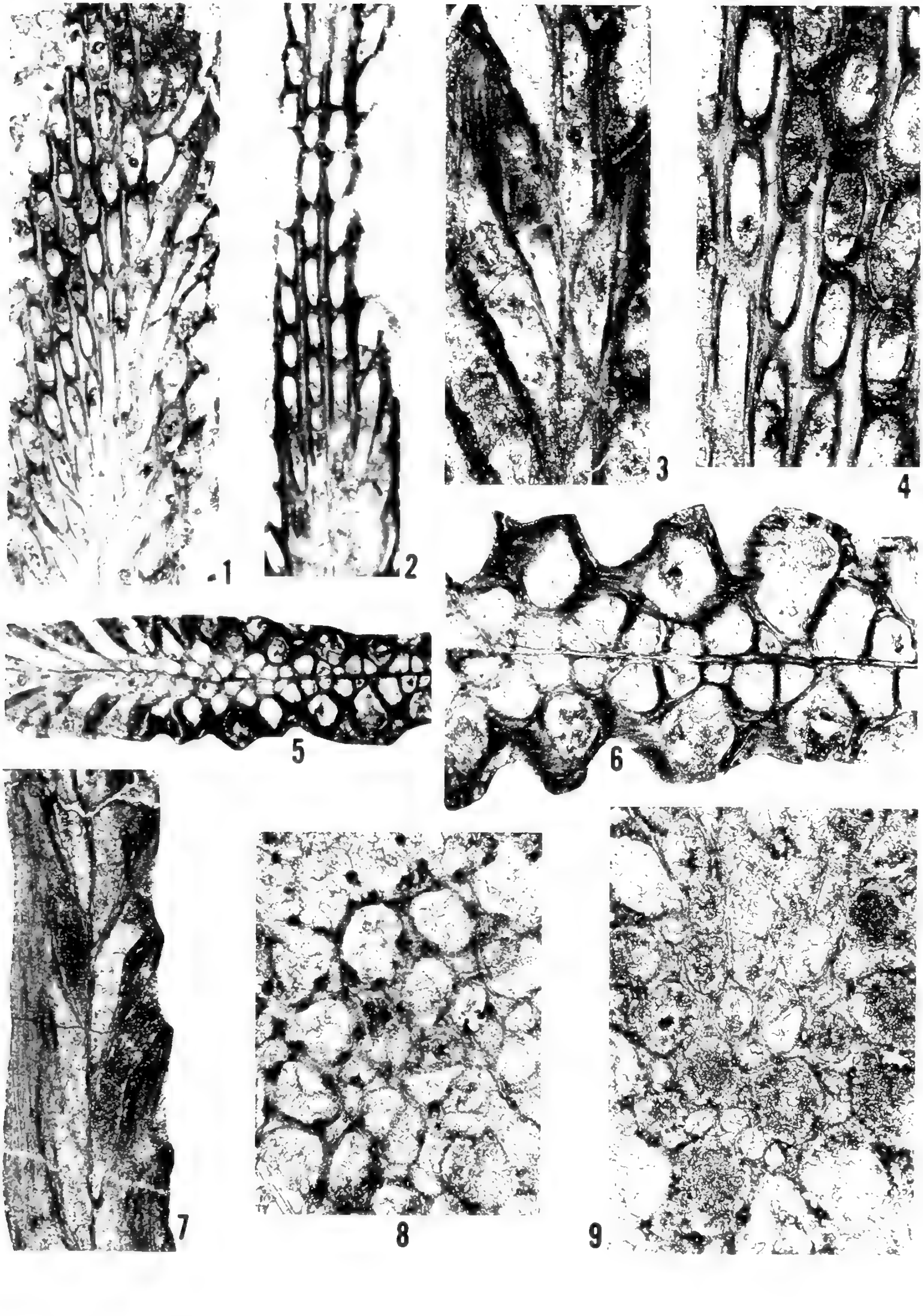
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PLATE 5

***Pseudohornera*? sp.** p. 124

FIGS. 1, 6. Oblique tangential-longitudinal section. PD. 4408. ×50 and ×20, respectively.

FIG. 2. Oblique section of branch enclosing a phylloporinid. PD. 4409. ×20.

***Mitoclemella*? sp. A** p. 120

FIG. 3. Zoarial surface. PD. 4419. ×10.

***Stictopora* sp.** p. 129

FIGS. 4, 10. Oblique tangential section. PD. 4410. ×20 and ×50, respectively.

Phylloporinid p. 132

FIG. 5. Transverse section displaying laminate wall structure. PD. 4411. ×50.

***Stictopora*? sp.** p. 129

FIG. 7. Transverse section. PD. 4412. ×50.

***Pachydictya* sp. A?** p. 127

FIG. 8. Oblique tangential section. PD. 4413. ×50.

***Pachydictya* sp. A?** p. 127

FIG. 9. Longitudinal section. PD. 4414. ×50.

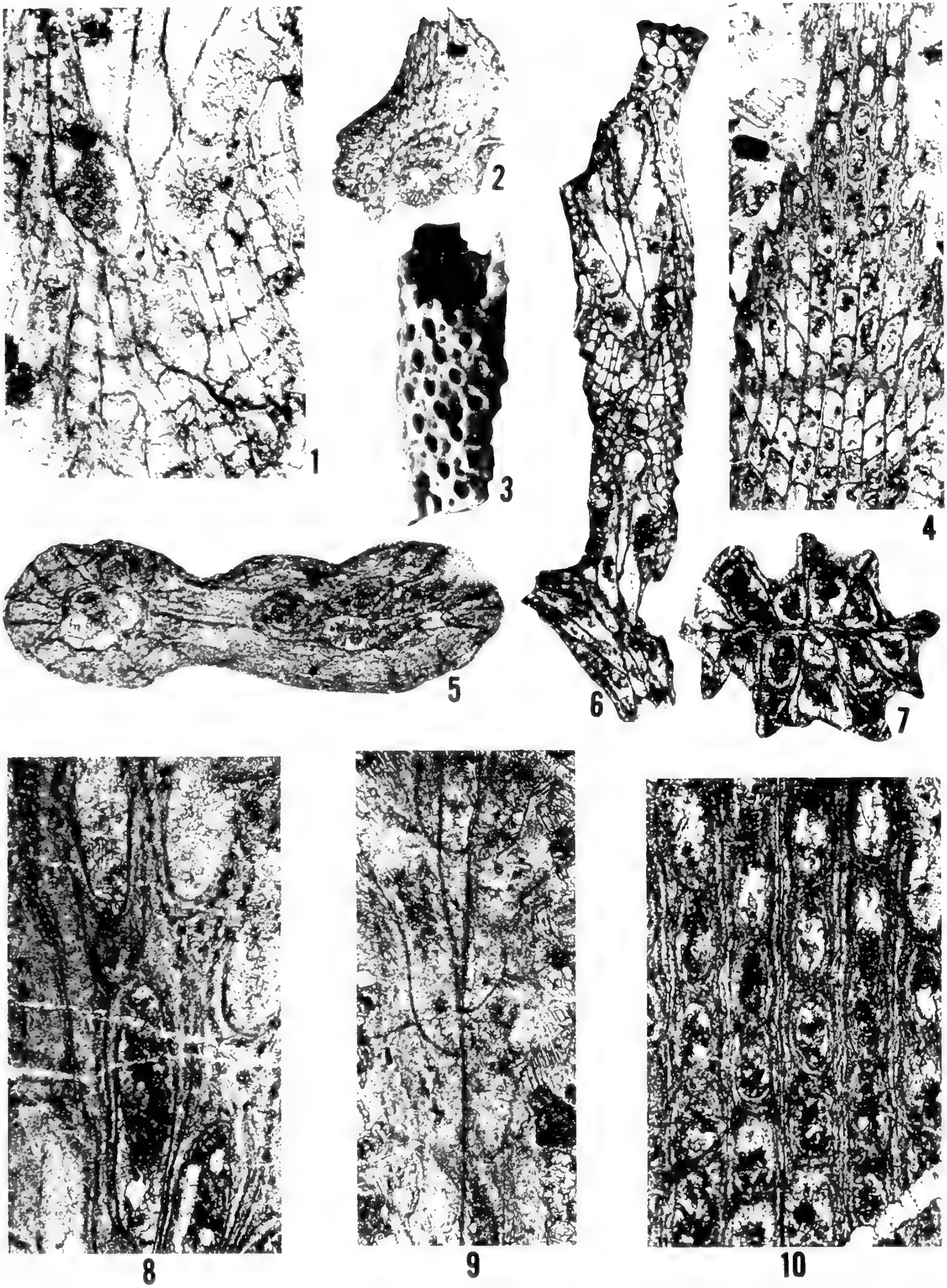
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PLATE 6

All figures ×10, except Fig. 4, ×50.

Calopora sp. A   p. 113

FIG. 1. Zoarial surface with zooecial openings and mesopores. PD. 4422.

Calopora sp. B   p. 115

FIG. 2. Zoarial surface with zooecial openings and mesopores. PD. 4423.

Penniretepora sp. A   p. 122

FIG. 3. Obverse side of main branch and several lateral branches showing zooecial openings. PD. 4424.

Helopora? sp.   p. 130

FIG. 4. Transverse section. PD. 4418.

Anaphragma portranense?   p. 111

FIG. 5. Zoarial surface. PD. 4425.

Enallopora sp. A   p. 119

FIGS. 6, 7. Obverse side of bifurcating colonies showing zooecial openings. PD. 4426 and PD. 4427, respectively.

Pseudohornera? sp. A   p. 124

FIG. 8. Obverse side of bifurcating branches with zooecial openings. PD. 4428.

Polyzoan? or ***Alga***?   p. 133

FIG. 9. Reticulate colony. PD. 4429.

Phylloporinid   p. 132

FIG. 10. Obverse side of reticulate zoarium showing zooecial openings. PD. 4430.

Mitoclemella? sp. A   p. 120

FIGS. 11, 12. Oblique zooecial openings on zoarial surface. PD. 4420 and PD. 4421, respectively.

Cf. ***Ichthyorachis*** sp.   p. 130

FIG. 13. Obverse side of main branch and several lateral branches with zooecial openings. PD. 4431.

Anaphragma portranense?   p. 111

FIG. 14. External view of colony. PD. 4432.

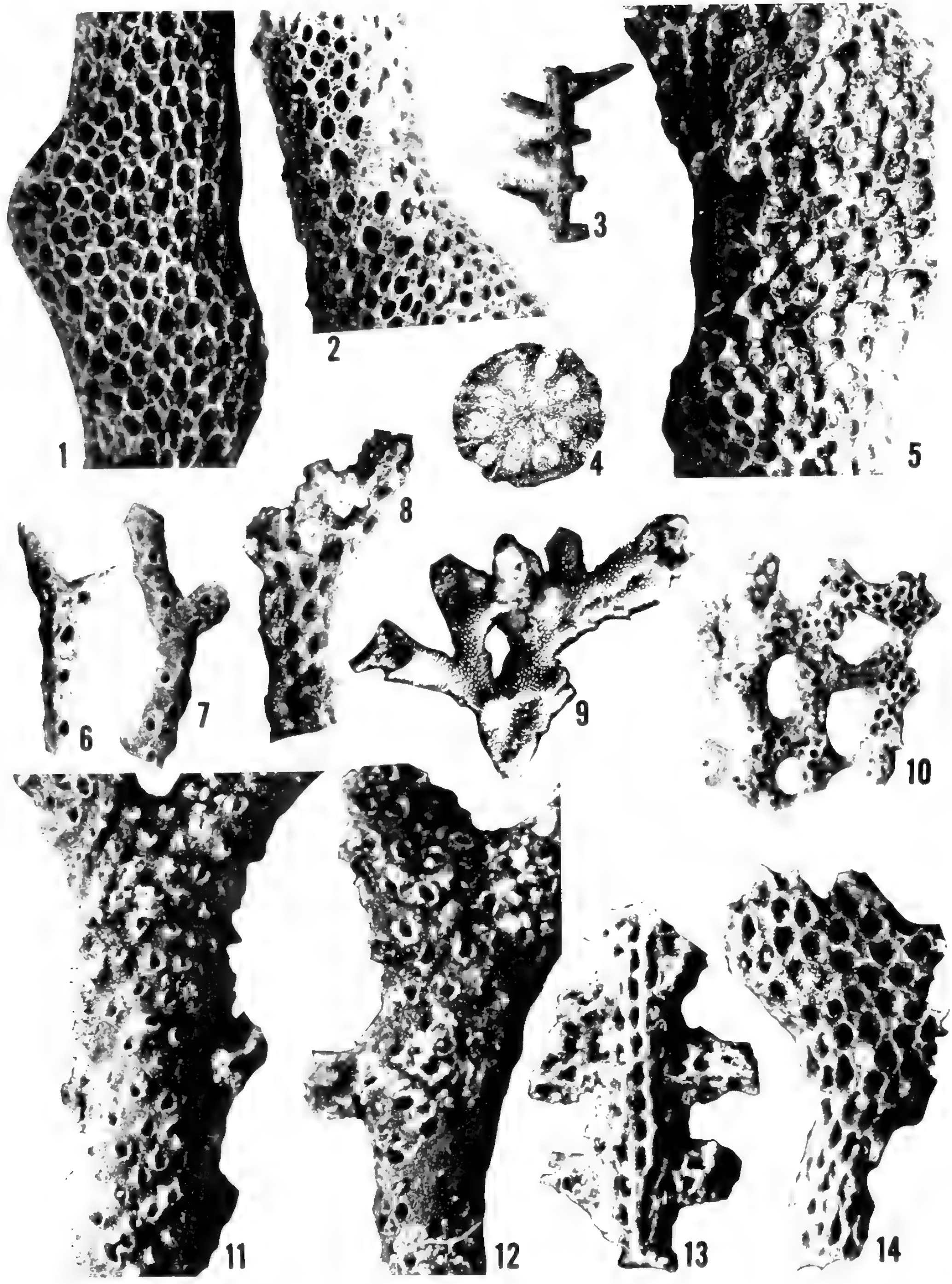
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PLATE 7

All figures ×10

Ptilodictya sp. A p. 125

FIG. 1. Zoarial surface showing direct and oblique zooecial openings. PD. 4433.

Stictopora sp. p. 129

FIG. 2. Zoarial surface with zooecial openings. PD. 4434.

Ptilodictya sp. B p. 126

FIG. 3. Zoarial surface of wide zoarial branch. PD. 4435.

Pseudohornera? sp. B p. 124

FIG. 4. Obverse surface showing zooecial tubes. PD. 4436.

Mitoclemella? sp. A p. 120

FIG. 5. Slender cylindrical stem with oblique zooecial openings. PD. 4437.

Pseudohornera? sp. A p. 124

FIG. 6. Obverse surface with zooecial openings. PD. 4438.

Helopora? sp. p. 130

FIG. 7. Bifurcating colony with oblique zooecial openings. PD. 4439.

Nematopora? sp. p. 131

FIG. 8. Slender cylindrical stem with elongate zooecial openings. PD. 4440.

Clonopora? sp. p. 132

FIG. 9. Isolated diverging zooecial tubes. PD. 4441.

Pachydictya sp. A p. 127

FIG. 10. Part of zoarial surface of branch. PD. 4442.

Pachydictya sp. B p. 128

FIG. 11. Part of zoarial surface of branch. PD. 4443.

Amplexopora? sp. p. 117

FIG. 12. Zoarial surface of fragment of colony. PD. 4444.

Polyzoan? or ***Alga***? p. 133

FIG. 13. Reticulate colony. PD. 4445.

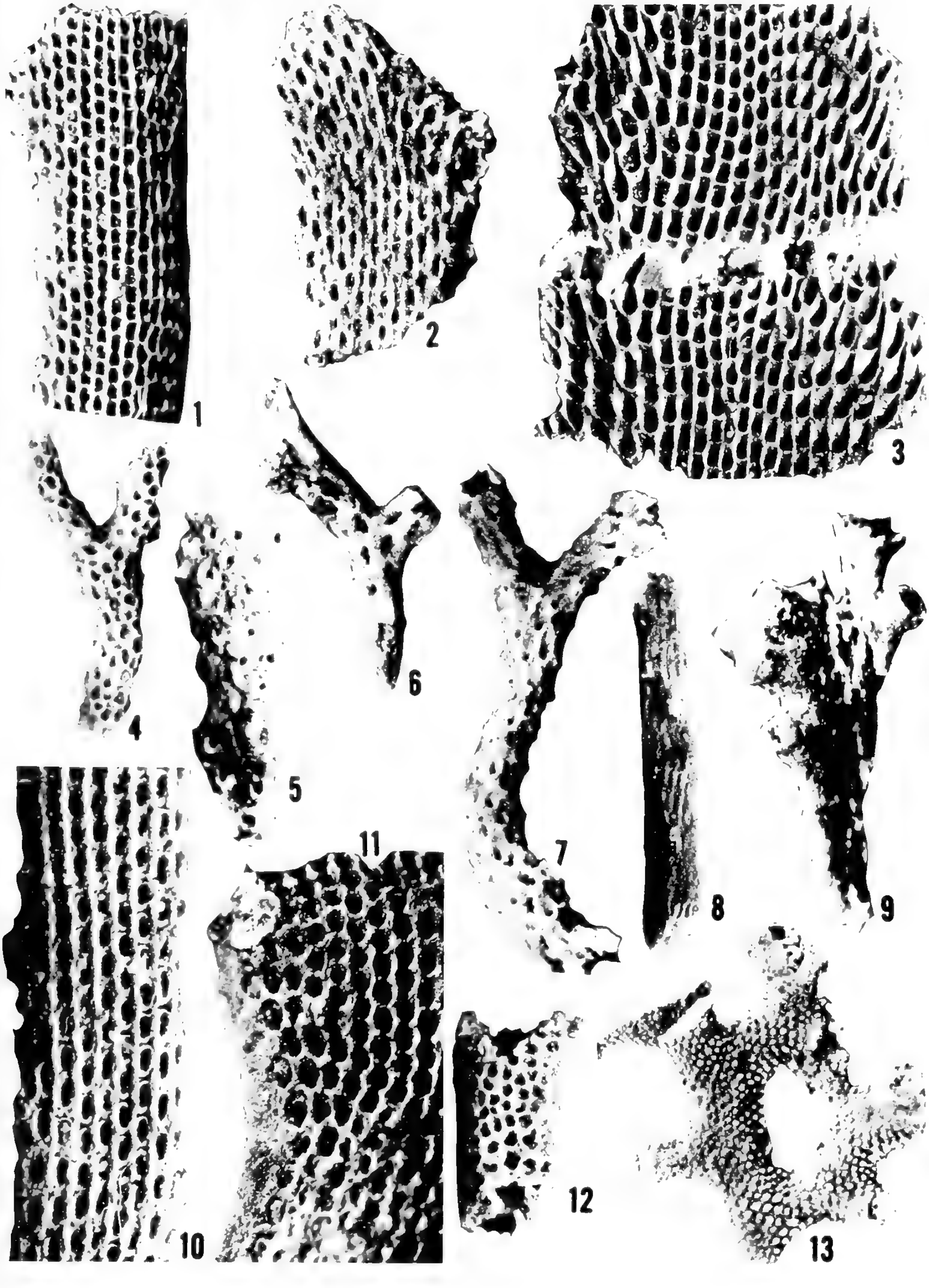
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PLATE 8

Discosparsa? sp. p. 133

FIGS. 1, 2. View of calyx of colony showing zooecial tubes aggregated together in cup-like form. PD. 4468, 4469, respectively. ×5.

FIGS. 3, 7. External aspect of colony showing a small part of external wall of shallow cup-like colony. PD. 4469, 4468, respectively. ×5.

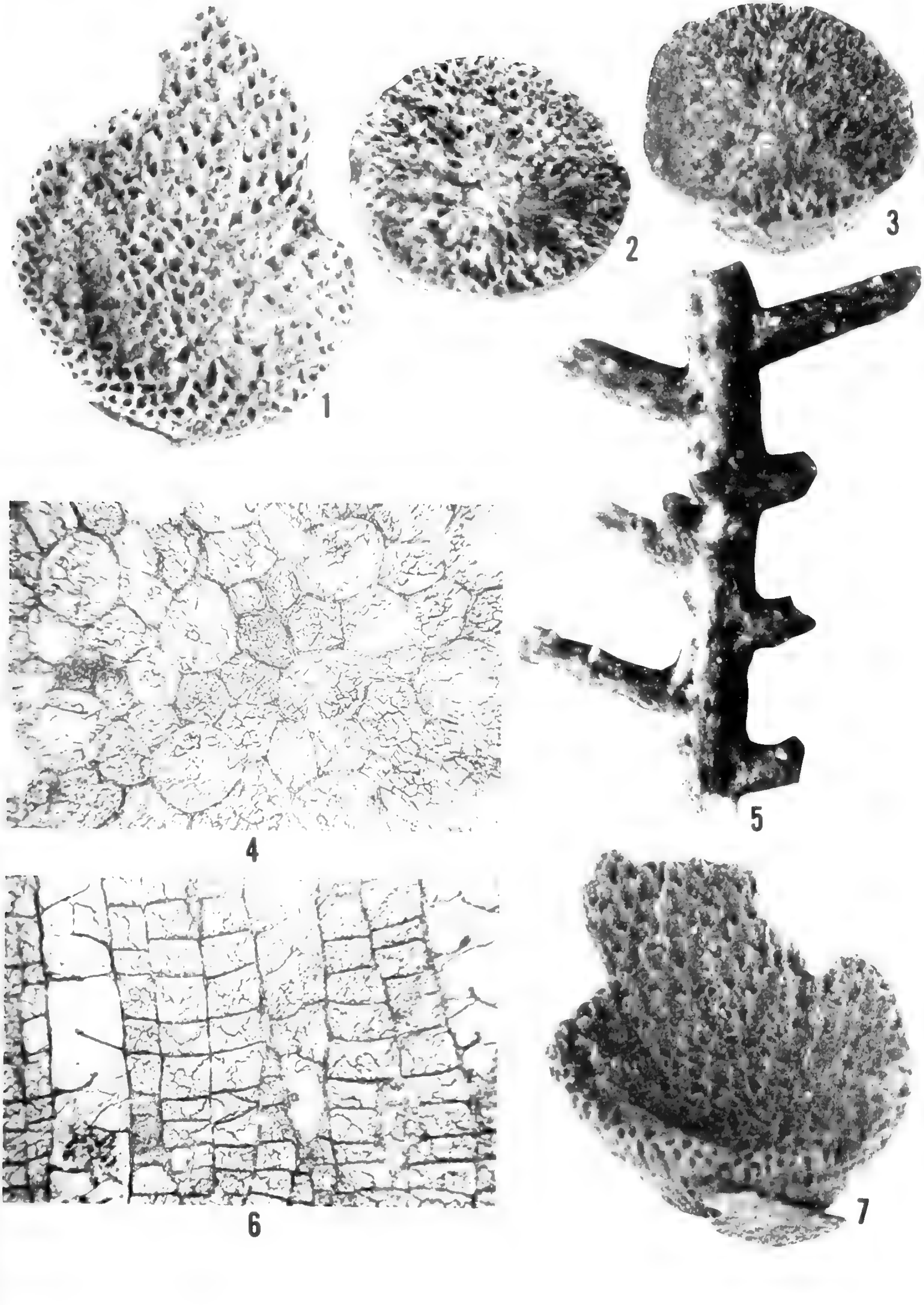
Phragmopora multiporatum Bassler p. 117

FIG. 4. Tangential section showing round zooecial openings and polygonal mesopores. Holotype, USNM 57421. ×50.

FIG. 6. Longitudinal section of same specimen showing zooecial tubes with hemiphragms and mesopores with diaphragms. ×50.

Penniretepora sp. A p. 112

FIG. 5. Obverse surface of pinnate colony with zooecial openings on steeply sloping surfaces. PD. 4424. ×30.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NATURAL

FRUITING ORGANS FROM THE MORRISON FORMATION OF UTAH, U.S.A.

M. E. J. CHANDLER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 12 No. 4
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FRUITING ORGANS FROM THE MORRISON FORMATION OF UTAH, U.S.A.

BY

MARJORIE E. J. CHANDLER

Pp. 137–171 ; 12 *Plates* ; 46 *Text-figures*

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FRUITING ORGANS FROM THE MORRISON FORMATION OF UTAH, U.S.A.

By M. E. J. CHANDLER

SYNOPSIS

This paper deals with a number of interesting plant remains from the Morrison Formation of Utah, U.S.A. Some are represented by numerous individuals, others by only one or a few. Three of the recorded genera (*Behuninia, Jensensispermum, Hillistrobus*) are new and five new species are described and figured.

With the exception of *Sequoia* all the plants appear to be extinct and are not comparable with any vegetation hitherto described ; they differ from all Mesozoic plants previously known, not only in their characters but in their preservation as solid entities. Angiosperms appear to be absent in spite of superficial resemblances to them in a few cases.

The seed, *Jensensispermum redmondi* gen. et sp. n., is remarkable for a combination of characters which distinguish it from any recognizable family viz. a conspicuous embryo vesicle centrally placed in the massive endosperm, a complex chalazal structure partly embedded in endosperm and a cycad-like hilar cavity. The toadstool-like seeds of *Carpolithus radiatus* sp. n. have features in common with *Jensensispermum*. Both are of a type entirely unknown today.

The geology and mode of occurrence of the specimens are briefly outlined in a foreword by Mr. J. A. Jensen who regards the age of the parent deposit as probably late Jurassic. *Sequoia*, common in the Cretaceous and rare in the Jurassic, has no contribution to make on the question of age. The aspect of the flora is, however, essentially Mesozoic.

FOREWORD

By JAMES A. JENSEN, Curator

Geology Department, Brigham Young University, Provo, Utah, U.S.A.

Geology and Occurrence

THE material described herein was first discovered by Homer and Joanne Behunin of Redmond, Utah, and many of the specimens used in this study were donated by them. The interesting variety available from this locality is due to their patient diligence in collecting. Grateful acknowledgement is hereby made of their willing co-operation.

The material studied was collected from a single locality (east of Last Chance road leaving highway U10 near Fremont Junction) about five miles east of Willow Springs, Emery County, Utah.

Its geologic age is placed in the Brushy Basin member of the Morrison Formation (by Bennett (1955)).

The specimens occur as resistant casts of the original organic structures, such as seeds, cones, buds etc., and were found weathered out of a fine grained, grey, limey sandstone. Being simply casts of external surfaces, all internal structures so valuable to morphological studies are missing.

No leaves were evident in the matrix but other plant fragments of various kinds were abundant including wood sections ranging in size from small twigs up to pieces about 130 mm. in diameter and about 1·5 metres long. One area in the deposit contained numerous tuber-like objects which, owing to their concentration, appear to be at, or very near, their point of origin. Most of the material appears to have been subjected to disturbance during the process of fossilization.

Several large dinosaur bones were present but due to the activity of amateur bone collectors there is little evidence left to suggest the mode of their introduction into the area.

The presence of numerous freshwater Gastropods in an adjacent area and a large stream channel deposit in another, divided by the fossil plant deposit, suggests that the sedimentary environment consisted of a shallow pond, or lake, separated from a large stream by an elevated area.

The general region was one of flood-plain activity, so common in Morrison times, and was no doubt low in elevation. It was probably less than 300 metres above sea level although the present elevation is about 1650 metres. Moderate humidity and a warm climate are evident but conditions were far from those of a coal swamp.

The deposit is generally from 0·3 to 0·5 metres in depth and is somewhat resistant which results in its occurrence on the tops of two small hills. Modern erosion has removed the intervening area.

The discovery of several new genera and species of plants in these beds in central Utah is of great significance. They are very important to the study of Palaeoecology and may have some contribution to make to the problem of why dinosaurs were eventually unsuccessful in their environment.

The flora of the Jurassic period in the western United States has been described largely from formations other than those which contain the best fauna. Very little has been published about the varied plant forms of the Morrison formation (apart from Cycad stems) since conditions which preserved animal skeletons so well at that time were unfavourable for detailed plant preservation.

INTRODUCTION

The small group of plants here described has been entrusted to me by Mr. James A. Jensen of Brigham Young University, Provo, Utah, who with Mr. Behunin collected the bulk of the material. As I am wholly unacquainted with the formation, Mr. Jensen has also kindly contributed the foregoing account of the geology of the parent deposit and the mode of occurrence of the fossils. He and I are both indebted to Professor D. I. Axelrod for putting us in contact with one another and thereby making this investigation possible. I am personally indebted also to Professor T. M. Harris for sparing time to look at some of the more outstanding specimens. His opinion

on Mesozoic plants is worth infinitely more than my own. My experience of palaeobotany has been almost entirely restricted to the Tertiary. The sole justification, therefore, for attempting a study of these older fossils is that in their superficial appearance some of them bear a misleading resemblance to Angiosperms, while their preservation as solid entities, can be interpreted in the light of many years of research on similarly preserved Tertiary fruiting organs. The majority of Mesozoic compressions call for a different approach and a radically different technique. The best characterized and most abundant forms from Utah are not only entirely new to me but to Professor Harris also. They may, therefore, safely be assumed to be new genera and species the possible affinities of which are discussed in some detail in the systematic section which follows.

Despite the large quantities of specimens examined distinct forms are few, only seven species being sufficiently well characterized, having regard to the mode of preservation, for satisfactory or even partial determination or diagnosis. Among them is a species of *Sequoia*, not named specifically on account of its poor condition but showing on the surface of the cones typical *Sequoia* features. A detached small fragment of Conifer foliage may, or may not, belong to these cones but more probably to the species *Hillistrobus axelrodi* (see below). While *Sequoia* is a common Cretaceous genus in North America (Chaney 1951 : 188) it apparently occurs sparsely in the Jurassic elsewhere. Endo (1951 : 228 text-figs. 1, 2 ; with foreword by Chaney) described as *Sequoia jeholensis* a bifacial branchlet from the *Lycoptera* beds of Lingyuan, Jehol, in South Manchuria. These beds were stated to be of Upper or Middle Jurassic age. A cone of somewhat uncertain affinity was earlier recorded from the Upper Jurassic of the Boulogne area (Fliche & Zeiller 1904 : 787) under the name *Sequoia problematica*, but of it Endo writes (1951 : 230) " the relationship to *Sequoia* has not been demonstrated ". Hence while it may be possible for *Sequoia* to occur in Jurassic beds it should also be borne in mind that " the Morrison Formation is in the upper part of the Jurassic if not at its very top " while " the boundary of the Jurassic and Cretaceous in this part of the World [Utah] is a subject of some mild controversy " (Jensen, ex. lit., 18.2.64).

A second coniferous cone, represented by several specimens, may also belong to the Taxodiaceae. Professor Harris pointed out that there is some resemblance between these specimens and *Sphenolepis kurrianus* (Dunker) Schenk (Harris 1953 : 6, pls. 1, 2) but added that the limits of this species are ill-defined. Owing to the type of preservation of the Utah cones some of the diagnostic characters used in defining *Sphenolepis* and an allied genus *Elatides* Heer are not visible even if present. There is some reason to think that they could be male cones. Their external appearance is so distinctive that it seems justifiable to give them a name although their diagnosis is necessarily very incomplete. They are described as *Hillistrobus axelrodi*. This name is a tribute to Dr. A. J. Hill, the Dean of the College of Engineering (including Geology) at Brigham Young University. He and his wife have visited the site and have shown great interest in this work. The specific name *axelrodi* is after Professor D. I. Axelrod because of his part in introducing the writer to Mr. Jensen and to these plant remains.

Two other cones are too obscure for diagnosis but clearly different from the foregoing. They have therefore been illustrated and briefly described although no attempt has been made to name them.

There are only two other species which can be assigned, even approximately, to a systematic position and they, fortunately, are abundant. One of these, *Behuninia joannei* gen. et. sp. n. shows seeds borne on a dorsiventral sporophyll and may well belong to the Cycadales. The other, *Jensensispermum redmondi* gen. et. sp. n. is a peculiar albuminous seed whose foliage and mode of growth on the infructescence are both at present unknown. Although it shows some Cycadean features, for reasons to be discussed it cannot be placed in any recognized family. Its position must, therefore, be regarded as extremely doubtful but it is grouped provisionally with the Cycadophyta. The complex character of its chalaza excludes it from Cycadales and it is not possible to refer it to any family hitherto defined (cf. p. 154). The first of these two new genera is called after the initial discoverer of the plant material, Mr. H. Behunin and his wife Joanne. The fact that Mr. Behunin keeps a rock shop in the village of Redmond, Utah explains the specific name of the seeds described as *Jensensispermum* after James A. Jensen himself.

A fragment of a dorsiventral sporophyll with one broken partially embedded seed, although too imperfect for certain determination, has also been referred provisionally to Cycadophyta. The presence of Cycadaceous fruiting material in the Morrison is to be expected in view of the abundant Cycad stems long known to occur in Wyoming (Ward 1899 : 521–958, pls. 57–172 ; 1900 : 253–300 ; 1906 : 179–203, pls. 46–63 ; Wieland 1906, 1916).

Two other plants are named *Carpolithus provoensis* and *Carpolithus* sp. (65, 66). With no knowledge whatsoever of their internal structure or organization it is impossible to form a sound opinion of their true affinity. These specimens are figured and described without any attempt to relate them to a Class or Family. Some figures by Andrews (1963 : 927, 929, text-figs. 4–9, 15–19) of Lower and Upper Carboniferous Pteridosperm seeds and cupules suggest that they could be Pteridosperms or descendants of that group. Despite the fact that one of them bears a superficial resemblance to an Angiosperm berry, while *Jensensispermum* shows features which recall seeds of Sapindaceae, there are no grounds for regarding either as Angiosperms. In the latter case there are definite reasons for dissociating them from Sapindaceae.

Similarly unsatisfactory for determination are some peltate flattened circular heads with radial furrows and nerves. They are described and figured as *Carpolithus radiatus*. Certain of their seed characters suggest alliance with *Jensensispermum*. A large detached thorn cannot be placed. It is not even possible to say whether it has, or has not, any connection with one or other of the species seen. Evidence of its relationship is entirely lacking. This is also true of a few longitudinally ridged and furrowed elongate but obscure bodies with enlarged basal attachment (?) (Pl. 11, figs. 135–145). There is nothing to indicate whether they belong to higher or lower plants but in the light of Andrews' figures of cupules, quoted above, a Pteridosperm ancestry is perhaps not excluded.

In addition to the above forms which may all belong to the higher plants, there are innumerable subglobular, irregularly shaped and sometimes flattened and subcircular bodies with few distinctive features which could be Cryptogamous. Some of them show a clearly defined concentric structure, others a radial arrangement, others evidence of both, while many show form only and no structure whatsoever. In view of their ill-defined characters, although numerically important, only a few are figured and briefly described without naming or classification. Further discoveries may ultimately make it possible to determine their affinities. Meanwhile, it seems inadvisable to risk discrediting the work which is based on definite diagnostic features in other specimens by any attempt to classify these. Professor C. G. C. Chesters kindly examined a few of the better preserved examples but was unable to accept a suggestion that they might be fungi. Their association with masses of broken partly disintegrating wood to which in one or two cases they are attached (V.51815–16) may indicate such an affinity but an algal relationship is equally possible. There the matter must rest for the present.

The quantities of wood fragments ranging from small twigs to branches several cms. in diameter of which about five hundred specimens have been seen is one of the striking features of these plant beds. Mr. Jensen writes also of large trunks which occur. Unfortunately there is no internal structure to help in the determination of most of this material and even the surface features are commonly ill-preserved. Some of the better fragments do however show a characteristic surface with numerous discontinuous sharp subparallel furrows like those described in *Behuninia* and *Carpolithus provoensis* (pp. 145, 162, Pl. 1, figs. 4, 5; Pl. 9, fig. 90). The furrows may indicate partially exposed fibro-vascular strands showing at the surface intermittently. Possibly their disposition is a family or group characteristic. Whatever the relationship the size of many of these fragments points to parent plants with the habit of shrubs or trees.

Although so little is known with certainty these fragmentary plants are of considerable importance. The fruiting organs are definitely new. The type of preservation is apparently unusual in the Jurassic. They can be removed, after weathering, from the matrix and examined " in the round ". The crystalline preservation is responsible for the lack of detailed information. The original living organs were probably buried in quickly accumulated sediments which consolidated rapidly around them. Subsequently the organic entities appear to have decayed while calcium carbonate, silica or a mixture of both have infiltrated in solution into the hollow moulds and surrounding matrix. As the mineral crystallized out they reproduced the superficial features of the specimens from the impressions on the hollows. Thus the fossils would seem to be internal crystalline casts of external moulds of plant remains, whether fruiting organs of higher plants, wood, or Cryptograms. This explains the absence of organic structure especially inside the cast. When sectioned they are consistently crystalline throughout. There is no hint of mineral replacement of actual tissues cell by cell as in the Tertiary London Clay fruits and seeds. Even superficial cell impressions can scarcely be said to exist perhaps because the matrix was not fine enough to reproduce them faithfully on the

hollow moulds so that they could not be transferred to the surface of the casts. All that is normally shown are the macroscopic features visible on the exposed surfaces of the specimens when they were buried. When, therefore, a part or the whole of an outer integument or epidermis had been torn away or abraded prior to fossilization, fibres or other structures which would have been hidden in a perfect specimen were exposed superficially and are reproduced. Again a film of matrix penetrating along a crack or fracture in a specimen may have shown detail now reproduced in calcite or silica. Such a film could then afford a rare, ill-defined, glimpse of structures or organs otherwise completely unknown. It is perhaps under some such conditions that one now fractured cone of *Sequoia* appears to show obscurely the position and size of the seeds on the scales (Pl. 8, fig. 78). Normally, however, it is a useless and frustrating task to section these casts in the hope of revealing internal organic structures. There are no compressed coats or cuticles as in many Mesozoic plant remains, so that the wealth of detail available in such cases is lacking wholly in the Utah fossils. This factor of preservation means that important characters and coats in the fossils and the relation of these coats to one another cannot always be determined by direct observation but must be discovered by processes of induction. This of course adds to the difficulty of understanding the material. The distinctive macroscopic features in some of the species nevertheless make their study well worthwhile.

For determining the chemical composition of typical specimens thanks are due to the Mineralogical Department of the British Museum (Natural History). To the Director of the Royal Botanic Gardens, Kew, I owe the opportunity of examining in detail a number of Cycadaceous seeds both fresh and dried. Dr. K. I. M. Chesters has kindly typed the manuscript and has made valuable criticisms, Mr. G. Elliott has examined those specimens thought to be algae. The authorities of the Geological Department of the Brigham Young University, Provo, Utah have generously presented a large number of specimens to the British Museum (Natural History).

SYSTEMATIC DESCRIPTIONS

In the descriptions which follow, numbers in brackets refer to specimens which give evidence of special points described under each species. In every case the types have been returned to Utah. These and other specimens at Provo are indicated by arabic serial numbers without prefix. Those in the British Museum (Natural History) are indicated by a V. followed by the registered number.

The fragmentary character of the *Behuninia* sporophylls and the isolated condition of the seeds of *Jensensispermum* have made the interpretation of this obscure material rather difficult. Detailed comparison of as many specimens as possible has been essential. Only in this way could the diagnostic characters be detected, the connection between one specimen and another be established and a reconstruction from the detached remains be made. To illustrate adequately the features recognized by such methods it has been necessary to select a number of syntypes connected one with another by features in common. No single holotype in such material can provide adequate comprehensive evidence. For example differently abraded specimens

clearly linked by their major characters may show important successive coats or cavities which are not all visible in any one specimen. In the case of *Behuninia* a number of sporophyll fragments are needed to illustrate the difference between younger distally borne seeds (1, 2) and older ones (5, 6) which, having been more proximally situated, differ somewhat in appearance.

PLANT LIST

Group	Family	Genus and Species
Cycadophyta .	Cycadales .	*Behuninia joannei* gen. et sp. n.
		Genus ?
Cycadophyta ? .	Family ? . .	*Jensensispermum redmondi* gen. et sp. n.
Gymnospermae		
Coniferales .	Taxodineae .	*Sequoia* sp.
	Taxodineae ? .	*Hillistrobus axelrodi* gen. et sp. n.
		Genera ?
Incertae Sedis .		*Carpolithus provoensis* sp. n.
		Carpolithus radiatus sp. n.
		Carpolithus spp.
		Unknown plant bodies or organs and much undetermined broken and partially shredded wood.

CYCADOPHYTA

Family CYCADALES

Genus *BEHUNINIA* nov.

DIAGNOSIS. Orthotropous albuminous seeds arranged in opposite or sub-opposite pairs on upper surface of dorsiventral sporophyll extending to distal extremity. Embryo-vesicles two, the more conspicuous terminal, the other lateral on upper surface below middle of seed.

TYPE SPECIES. *Behuninia joannei* gen. et sp. n.

Behuninia joannei gen. et sp. n.

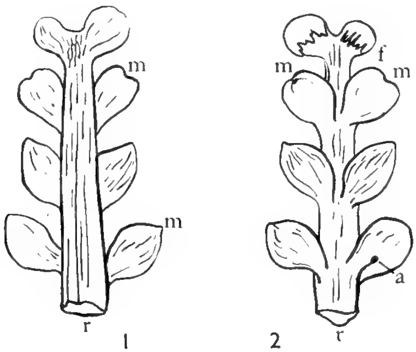
(Pls. 1–4, figs. 1–43 ; Text- figs. 1–12)

DIAGNOSIS. That of the genus.

SYNTYPES. Brigham Young University, Utah, Nos. 1, 2, 4, 5, 7–10.

DESCRIPTION. *Megasporophyll.* Dorsiventral (bifacial) bearing seeds in opposite or sub-opposite pairs extending to the tip. Seeds inclined at acute angles to the rachis arising on its upper surface and projecting laterally beyond its edges (4, 5, 19, V.51594) (Pls. 1, 2, figs. 4, 5, 9–14 ; Text-figs. 1–4). Those of each pair so closely adpressed to the rachis at their proximal ends that, when detached, they show a facet in the proximal half on the lower side (6, 9, 10, 15, V.51591) (Pls. 3, 4, figs. 22, 25, 35, 41 ; Text-figs. 5, 8, 11). Sometimes a narrow tract of sporophyll separates them along the middle of the rachis the upper surface of which shows a few sub-parallel discontinuous longitudinal furrows (1, 4). When viewed from below the

seeds are separated and their proximal ends are hidden by the prominent, broad, longitudinally ridged rachis itself (4, 5, 8). (Pls. 1, 2, figs. 5, 11, 14; Text-fig. 1). The distal end of the sporophylls may be incurved (? over abortive or young seeds) the free terminations being dissected (1) (Pl. 1, fig. 1; Text-fig. 2). On the lower surface between the seeds conspicuous, discontinuous, sub-parallel furrows indicate nerves, in places connected by transverse branches arising at wide angles, giving a reticulate appearance (1) (Pl. 1, fig. 2). A similar surface due to longitudinal furrows is also preserved on certain broken bits of wood (V.51596) and on the fruiting organ *Carpolithus provoensis*. In some specimens of *Behuninia* (14, 15) sporophyll fragments bearing seeds have a flattened bract-like aspect on the lower side which is enhanced by the tendency shown by their conspicuous nerves to fork acutely (Pls. 2, 3, figs. 16,25; Text-fig. 4). The discontinuous character of the longitudinal

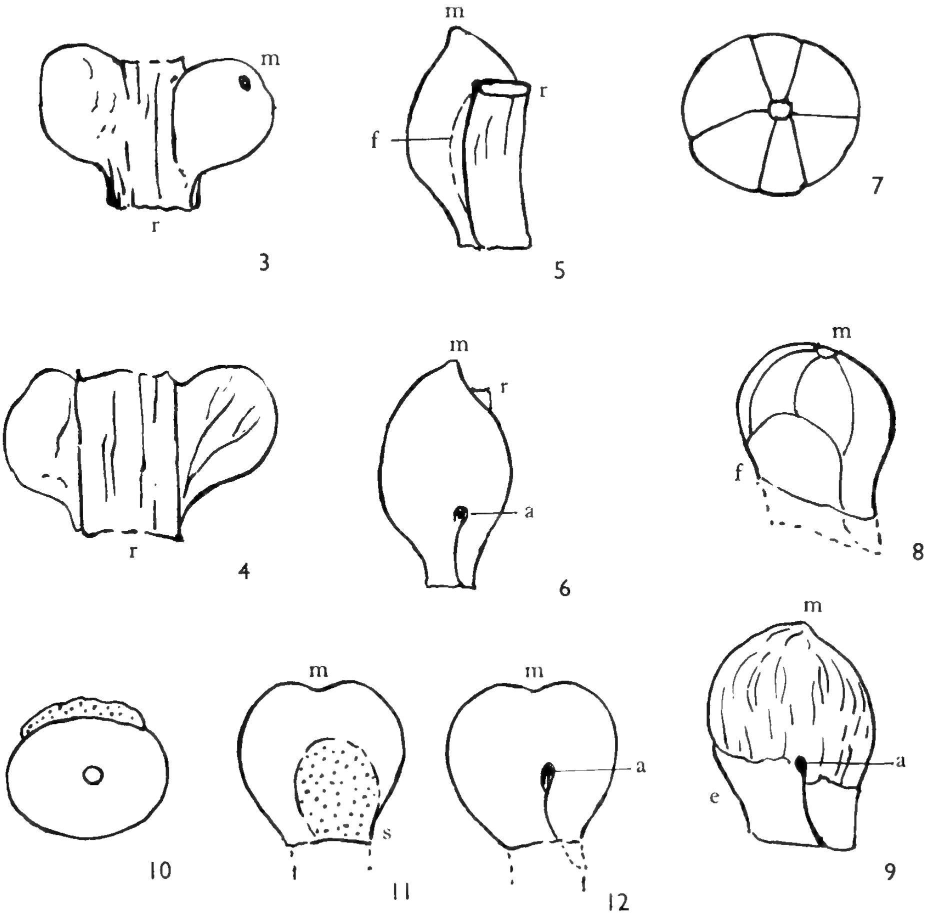


Figs. 1, 2. *Behuninia joannei* gen. et. sp. n. (Reconstruction). Macrosporophyll with pairs of seeds arising from upper side of rachis. Fig. 1, Lower surface with prominent rachis. Fig. 2, Upper surface showing how seeds arise. *m*, micropyle of fertile embryo; *a*, micropyle of abortive (?) lateral embryo; *r*, rachis; *f*, fringed ends of incurved most distal segments of sporophyll.

nerves suggests that they are unevenly sunk in the tissues of the sporophyll and are exposed at the surface by some measure of abrasion of the original organic entities. One fragment (19) shows what looks like a narrow thickened rim (? projecting lamina flanking the rachis) (Pl. 4, fig. 37). Some seeds (13) and small twig fragments (V.51597) which probably belong here display bud-like structures of about four segments surrounding a central aperture. These may be immature seeds or ovules. Length and maximum breadth of sporophyll unknown. Breadth of fragments with paired seeds 20 to 25 mm. (largest specimens preserved). Maximum breadth preserved of rachis about 5 to 7 mm. narrowing towards the distal end.

Seed. Varying somewhat in shape and size according to its position on the sporophyll. Younger distally placed seeds tend to be smaller and subglobular (1, 2, 3, V.51588). Older seeds are more elongate, obovoid or sub-pyriform when the integument is preserved, but usually show some measure of dorsiventral compression

(4, 5, 19). Unabraded seeds are often pointed distally. One or two large much inflated subglobular seeds, 15 or 16 mm. long and broad (7, V.51595) are not quite complete at the proximal end. A few of the larger seeds, not necessarily fully mature since they appear to have been soft and crushable, are more attenuated at the proximal end (17, 18). Possibly they grew further down the sporophyll and projected more conspicuously beyond its edges. Such seeds (Pl. 3, figs. 30–33) are smooth externally as if less abraded than the more rugose specimens to be described (Pl. 2, figs. 17, 18; Text-fig. 9). One of the smooth seeds (17) shows the micropyle as a transverse slit (Pl. 3, fig. 31). Another (18) gives an appearance of two closely adjacent pores of which the significance is not clear. Seeds which had been abraded before fossilization so that all trace of pulp was removed show the micropyle very clearly. Thus a smooth inflated well developed specimen (10) (Pl. 3, figs. 21, 22; Text-figs. 7, 8) has a sharply defined circular scar against which clearly marked straight unbranched longitudinal nerves terminate. These nerves arise at the base of the seed on the upper surface. On the lower they can be traced upwards from the margin of the basilateral facet. The rigid smooth appearance in this case suggests that a hard inner layer of the integument is exposed. A similar circular micropyle to which regularly spaced unbranched fibres converge over the external surface of the hard layer occurs in the living *Macrozamia douglasii* Hill from Queensland. In *Stangeria eriopus* (Kunze) there are straight longitudinal fibres from base to apex at the same level in the integument. Some of the fossil seeds are mineral replicas of endosperm which must have been exposed either by splitting of the integument or by a greater measure of abrasion (Pls. 2, 3, figs. 10–12, 23; Text-figs. 3, 4, 10–12). Upon the rounded end of this "endosperm" the terminal micropyle, marking the outer end of a fertile embryo-vesicle, is indicated by a deep circular depression (8, V.51593). A similar but slightly less conspicuous lateral depression on the upper surface just below the middle is seen on a few seeds and appears to indicate a second, perhaps abortive, embryo-vesicle. This is suggested by analogy with *Cycas revoluta* Linn. The position of this second vesicle appears to be constant in the fossil. Although best exposed on the endosperm replica it is visible in some instances on specimens with some of the integument preserved (9, V. 59591)(Pls. 2, 3, figs. 17, 18, 34; Text-figs. 6, 9) perhaps owing to drying, contraction and clinging of the closely adherent integument. The lateral vesicle is connected by a narrow clearly marked furrow with the proximal end of the seed (9, 20, V.51591) (Pls. 2, 3, figs. 18, 34; Text-figs. 6, 9, 12). The seeds are albuminous, orthotropous. Micropyle terminal, attachment basal. Nervation and rugosities of the surface normally longitudinally aligned but nerves on the lower surface may fork as described above. Some specimens show exceptionally well both the longitudinal simple nerves on the upper surface and the forked nerves on the lower surface (Pls. 3, 4, figs. 25, 41–43). Other specimens appear to have undergone further abrasion and dessication before fossilization. These show irregular longitudinal rugosities such as could be caused by repeated splitting on drying of thin pulpy tissues like those of Cycads. One seed (9) (Pl. 2, figs. 17, 18) shows the exposed pulp still covered at the base by part of an outer epidermal layer. All seeds show some evidence of the apical micropyle although



FIGS. 3–12. *Behuninia joannei* gen. et. sp. n. Figs. 3, 4. Pair of seeds attached to fragment of rachis. Fig. 3, Upper surface. Right hand seed, cast of endosperm with apical micropyle exposed by abrasion of testa. Fig. 4, Lower surface with longitudinally ridged rachis and branching nervation on one seed. Figs. 5, 6. Young seed still attached to rachis. Fig. 5, Lower surface. Fig. 6, Upper surface showing lateral depression, ? micropyle of abortive embryo, from which a distinct furrow passes to proximal end of seed. Figs. 7, 8. Detached seed with outer layers of testa abraded exposing simple fibres converging to micropyle on innermost layer. Fig. 7, Apex. Fig. 8, Lower surface with facet produced by pressure against rachis. Fig. 9, Seed with epidermis abraded above where irregular longitudinal ridges of contracted flesh are shown. Micropyle of abortive embryo and associated furrow seen below. Figs. 10–12. Internal cast of seed (= endosperm). Fig. 10, Apex with micropyle. Fig. 11, Lower surface with facet as in Fig. 8. Fig. 12, Upper surface with micropyle of abortive embryo as in figs. 6 and 9. *a*, abortive lateral embryo; *e*, remaining epidermis; *f*, facet; *m*, apical micropyle of fertile embryo; *r*, rachis; *s*, adherent matrix over the facet.

sometimes indicated only by the convergence of nerves or other tissues but sometimes by a visible aperture. It is by analogy with Cycadales that this has been interpreted as the micropyle. The basilateral furrow has a very slight sigmoidal curvature and separates a narrow, scarcely reflexed snout-like region on the outer side of the seed from a somewhat broader region nearer to the rachis. It could mark a rudimentary device for splitting the integument below the second embryo (9, 14, 20, V.51592) (Pl. 3, figs. 26–28, 34; Text-figs. 6, 9, 12). The snout-like region can be detected in many specimens even when the second embryo-vesicle is not exposed or reproduced on the cast. Distal seeds about 10 mm. long, 6·5 mm. in transverse diameter. Proximal seeds about 16 mm. long, 12 to 16 mm. in maximum diameter. These dimensions undoubtedly fall short of a maximum which would have been associated with the proximal end of the sporophyll but are the largest yet encountered.

Remarks. About seventy specimens including twenty with paired seeds still attached have been examined but foliage, male organs and *complete* female sporophylls are quite unknown. These last are always represented by short lengths with one or a pair of seeds attached so there is nothing to indicate their size when complete. By examining the extant fragments side by side it has been possible to reconstruct the form at least of their distal ends. There are also isolated detached seeds. Occasionally the two seeds of an attached pair are unequally developed. The pressure facets well exposed on detached fruits sometimes lie on the opposite side to the lateral embryo-vesicle, in part at least, but are sometimes in a plane at right angles to it.

The dorsiventral sporophyll with paired seeds arising from its upper surface suggests affinity with Cycadales of the *Cycas* type. With such a relationship Professor Harris expresses agreement and he has pointed out that the presence of seeds right to the tip of the sporophyll indicates a distinct type of Cycad. Further support for Cycadalean relationship is afforded by the orthotropous albuminous seed with terminal micropyle, longitudinal fibres as described and integument which may be fleshy in part. The fossil also differs from Recent genera in the apparently uniform position of the second lateral embryo-vesicle. It has therefore been necessary to institute a new generic name. It and the specific name are explained on p. 142. The broken condition of the elongate sporophyll accords with that of the wood so abundantly represented in the deposit. It is undoubtedly connected with the mode of accumulation of this plant débris.

Genus ?

(Pl. 4, figs. 44–46; Text-fig. 13)

Description. *Macrosporophyll.* Represented by a fragment of a dorsiventral thickened scale perhaps one lobe of a pair. A crenature probably directed towards the axis of a cone as in *Zamia* or *Ceratostigma* retains the remains of a seed seated within it. The distal end of the seed is missing. A possible reconstruction of the scale is shown in Text-fig. 13 where the unbroken lines show the specimen as it now appears, the broken lines the parts missing. The edge of the crenature forms a low rim conspicuously shallower on one surface than on the other (Pl. 4, figs. 44, 45) so as

to expose the margin of the seed lying in the hollow. Laterally the crenature is prolonged into projecting " claws " which help to grip the seed. The claw regarded as the outer one is shorter, bluntly rounded, more or less complete. The inner claw is broken so its true length is unknown (cf. Text-fig. 13). Surface of sporophyll rough as if much abraded but on the less shallow side of the crenature a few slight furrows are visible at right angles to the edge (Pl. 4, fig. 44). Breadth of broken edge of sporophyll about 11 by 8 mm., the maximum dimension lying parallel with the broad surface.

Seed. Broken transversely so that its complete length cannot be ascertained. The subelliptical section (Pl. 4, fig. 46) indicates a somewhat greater degree of inflation where it abuts on the shallower edge of the crenature and a less convex surface on the opposite side. The proximal part of the seed which remains suggests that it was

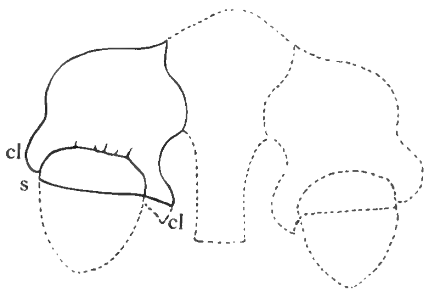


FIG. 13. Cycadales? Genus? Fragment of a dorsiventral thickened scale probably one lobe of a pair. Reconstruction as explained on p. 149. Broken lines represent missing parts. *s*, seed ; *cl*, claw-like prolongations of crenature which holds seed.

ovoid, with marginal angle having a narrow flattened marginal rim on the more inflated surface. On this surface there is an appreciable space between seed and crenature suggesting that pulpy tissues of the integument have been destroyed leaving exposed the hard bony layer. A similar space also exists on the less inflated surface of the seed but is there less obvious. The transverse section now exposed also indicates a shallow marginal furrow on the outer edge of the seed where it abuts on the outer claw of the crenature like the furrow sometimes seen in species of *Cycas*. The persistent hard integument varies in thickness from 1 to 2 mm. It is thickest where adjacent to the broken inner claw. Although the surface of the hard integument is so worn there are obscure indications of one or two longitudinal fibres on the less inflated side. Maximum breadth of seed parallel with the broad surface of the sporophyll, 14 mm. ; breadth at right angles to this surface, 12 mm. Length of fruit preserved above rim of crenature, 8 mm. on the more inflated side, 5 mm. on the opposite side.

AFFINITIES. The manner in which the seed is partly embedded in the sporophyll and the dorsiventral structure suggest a possible affinity with such Cycadales as *Zamia* or *Ceratostigma*. The form of the apex of the sporophyll is not known. The

reconstruction in Text-fig. 13 is not therefore intended as a portrait but serves to show that a Cycad-like structure is not impossible for the fragment which alone remains. In view of the scanty imperfect evidence the reference to Cycadales must be tentative only and no generic diagnosis can be based on this solitary fragment.

CYCADOPHYTA ?

Family ?

Genus *JENSENSISPERMUM* nov.

Diagnosis. Infructescence and fruit (if any) unknown. Seeds subovoid to subglobular, germinating by splitting at micropylar end. Integument probably pulpy. Funicle passing from hilum to chalaza through shallow hilar cavity. Hilar scar at inner end of cavity, large, gibbous, at right angles to longer axis of seed. Chalaza large, occupying approximately half of the seed connected at one end with hilar scar, penetrating into endosperm but later retracting and releasing it. Endosperm occupying other half of seed, turgid, at first hemispherical, later sometimes becoming conical by contraction, bearing a median navel-like embryo-scar.

Type species. *Jensensispermum redmondi* gen. et sp. n.

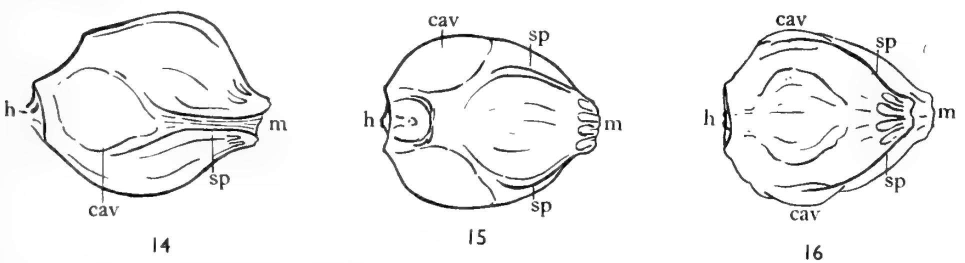
Jensensispermum redmondi gen. et sp. n.

(Pls. 5–7, figs. 47–74; Text-figs. 14–28)

Diagnosis. That of the genus.

Syntypes. Brigham Young University, Utah, Nos. 22–30.

Description. *Seed.* Subovoid when integument is preserved, pointed at micropyle (22, 23) which in some seeds is terminal on the longer axis opposite the hilum (22, 23) (Pl. 5, figs. 47, 51; Text-fig. 17) and in others terminal on the shorter axis (24) (V.51600; Text-figs. 18, 19). The position varies with the shape of the seed. The variations may perhaps be related to situation on an unknown inflorescence.

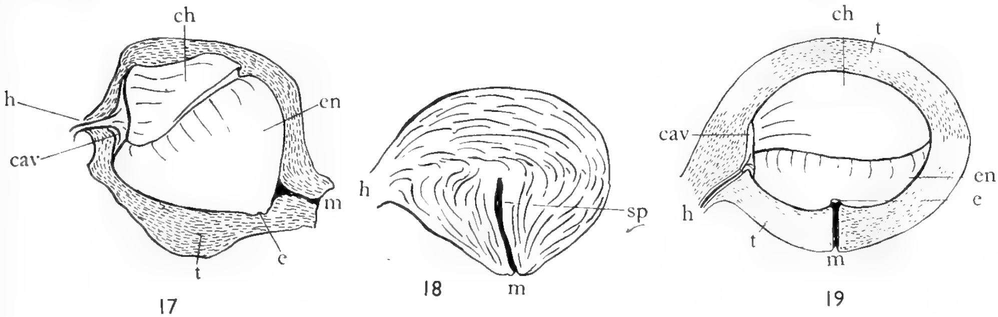


Figs. 14–16. *Jensensispermum redmondi* gen. et sp. n. Fig. 14. Specimen interpreted as seed with integument preserved, side. In this specimen micropyle is opposite hilum (based on 22). Fig. 15. Same, from chalazal side. Fig. 16. Same, from side with endosperm. *cav*, shallow superficial cavities now occupied by mineral casts, exposed by abrasion of epidermis; *h*, hilum; *m*, micropyle; *sp*, plane of weakness perhaps connected with germination.

Seeds tend to split transversely at the micropyle perhaps in connection with germination (23, V.51599) (Pl. 5, figs, 51, 52; Text-figs. 14, 18). One which may be a virtually perfect seed shows a pair of shallow superficial lateral cavities now occupied by mineral casts (22) (Text-figs. 14–16). The smooth well-defined surface of these casts indicates that the cavities were originally closed superficially so the former presence of an epidermis may be inferred. In many specimens remains of an inner pulpy layer of the integument have been exposed. The integument has become dried and shredded as in *Behuninia* (p. 147) and therefore appears rugose and somewhat fibrous in fossilization, the orientation of the ridges or fibres being from hilum to micropyle (23) (Pl. 5, fig. 51; Text-fig. 18). Such tissues must originally have covered the whole seed as they are seen on both sides (23) (Text-fig. 18) and when most complete they conceal the internal hilar scar. At the hilar end there is a small cavity. It is very shallow at right angles to the length of the seed and is traversed by the funicular fibres in their passage from the external hilum to the seed-cavity proper (Text-figs. 17, 19). Its existence is demonstrated by its internal cast in some specimens (28, V.51600) (Pls. 6, 7, figs. 62, 63, 74; Text-figs. 17, 19–22). It varies somewhat in size and form and at first sight suggests a slightly thickened hilar scar until its true nature as the mineral cast of a hilar cavity is understood.

The most frequent and conspicuous entity preserved is the subovoid internal cast of the seed-cavity itself. This is truncate at the hilar end by a large, gibbous, sunk scar at right angles to the longer axis of the seed. It marks the inner limit of the hilar cavity and is referred to above as the internal hilar scar. It is exposed when the cast of the hilar cavity is missing as is often the case (25) (Pl. 6, fig. 58; Text-figs. 23–25). The hilar scar may show apertures where the fibres of the funicle penetrated. Some are visible along the straight margin passing to the front part of the endosperm. Others are seen at the centre of the scar (25) (Pl. 6, fig. 58; Text-fig. 23). The seed-cast is divided along its major axis into two regions; the endosperm and the chalazal area. The endosperm is adjacent to the straight edge of the gibbous hilar scar and is commonly hemispherical (Pl. 6, figs. 56, 57, 61; Text-figs. 20, 21, 24, 25) more rarely hemipyriform and narrowed towards the hilum (24, V.51606). It normally has a smooth distended surface but in some specimens is puckered and somewhat contracted and conical as if it had begun to dry out (26, V.51613). It always bears a conspicuous, small navel-like circular scar sunk in a shallow median depression. As the integument is so often abraded the scar is a conspicuous feature. When it is best preserved it has a convex round centre like a pin-head (25, 30, 31, V.51601, V.51603) (Pls. 5–7, figs. 53, 56, 57, 61, 71, 72; Text-fig. 24). Occasionally the "pin-head" is partially or wholly extruded. By analogy with many Recent plants, more especially Cycadales and Palmae, this scar marks the point where the micropylar canal impinges on the endosperm. Such scars in Recent seeds indicate the presence of a superficial embryo-vesicle sunk in the endosperm and are here called the embryo-scar. Where the pulpy integument is partially preserved the embryo-scar may be concealed, but its position in such cases is indicated, as already noted, by the convergence towards it of the fibrous-looking pulp. The endosperm is very sharply delimited from the chalazal area (25, V.51600) (Pls. 5, 6, figs. 55, 62, 73; Text-figs.

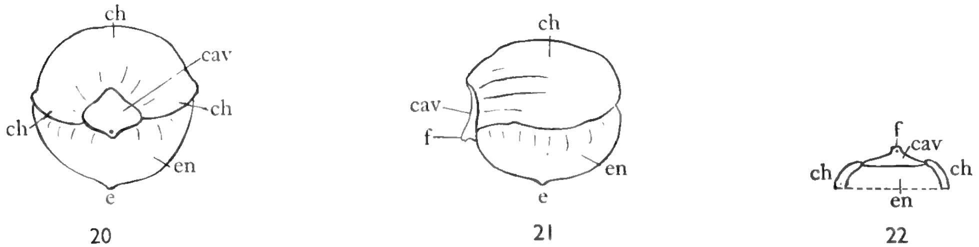
21, 23, 25) from whose margin striations due to fine lines of contraction, but also fine nerves diverge onto its surface. The nerves can be detected for a short distance only (29) (Pl. 7, fig. 68) and are best exposed when most of the chalazal area is missing. The endosperm evidently arises from and is firmly attached to the chalazal area which abuts upon the gibbous part of the hilar scar (Pl. 6, fig. 58 ; Text-fig. 23). In the less abraded seeds the area may be very thick (35). It commonly appears to overlap onto the endosperm and partly embrace it. It lies, of course, opposite to the micropyle. When present, the cast of the hilar-cavity slightly overlaps both halves of the seed (Text-figs. 17, 19, 20). In a few better preserved specimens the surface



FIGS. 17–19. *Jensensispermum redmondi* gen. et sp. n. Fig. 17. Seed as in Text-fig. 14 with micropyle opposite hilum depicted with pulpy integument removed on near side so as to expose internal cast. In this seed endosperm has become conical with embryo at point of cone. The chalazal area is somewhat shrunk and retracted. Integument reconstructed. Fig. 18. Seed with downward directed micropyle. Epidermis abraded exposing shredded dried pulpy integument. Fig. 19. Seed of similar shape to 18 but with pulp removed on near side as in 17. The endosperm is smoothly rounded and chalazal area unshrunk (integument reconstructed). *cav*, cavity at hilar end represented by a calcite cast through which funicle passes to inner side of hilar scar and chalazal area, *ch*. *e*, embryo scar in endosperm, *en*. *h*, hilar region ; *m*, micropyle ; *sp*, plane of splitting ; *t*, pulpy integument.

of the chalaza which lay in contact with the integument is smoothly finished and traversed by distinct separate longitudinal nerves arising at the edge of the hilar scar or from beneath the cast of the hilar cavity (28, V.51610). The nerves sometimes show branching and anastomozing producing raised areas, obscurely seen between the reticulations thus formed. More often, the smooth surface has been worn away exposing irregular rugose tissues (Pls. 6, 7, figs. 66, 70 ; Text-fig. 26). In many seeds the smooth surface is concealed by remains of the pulpy integument. Owing to different degrees of abrasion the chalazal area varies much in size relative to the endosperm. At its largest it occupies half to rather more than half of the total surface of the seed-cast. In other specimens it is proportionately reduced or it may be almost entirely worn away. Some (?) riper seeds show it retracted from the endosperm and in these it is much smaller, puckered or concentrically wrinkled, with its free margin thickened and raised (26) (Pl. 6, fig. 64 ; Text-fig. 17). It is in these last that the endosperm tends to be conical and contracted with the embryo-scar at the point of the cone. In a few specimens the endosperm appears to have been

released from the chalaza and its rear surface, thereby exposed, may be concave with adherent patches of tissue at the centre of the concavity only where the two halves were most intimately fused. The nerves are then seen radiating from the sharply defined margin of the concavity onto the endosperm. The patches of tissue described sometimes form a knob-like projection like the " shank " of a button represented by the endosperm itself (27, V.51602) (Pl. 7, figs. 69, 70 ; Text-figs. 27, 28). In some seeds that are detached from the chalaza the rear surface of the endosperm appears longitudinally puckered. Some specimens have the endosperm corroded but these can be recognized by the remains of the embryo vesicle which persists surrounded by a mere frill of endosperm when most of the rest of the seed has been destroyed.



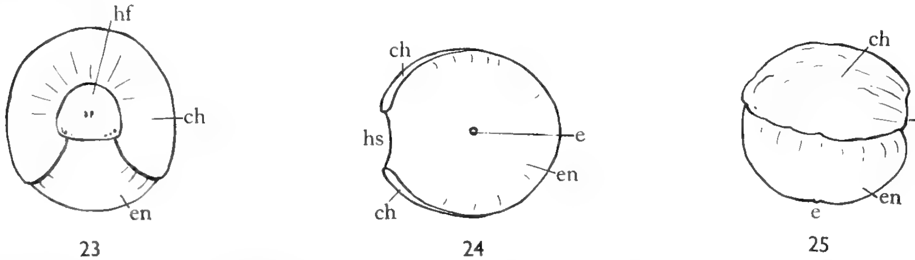
FIGS. 20–22. *Jensensispermum redmondi* gen. et sp. n. Fig. 20. Internal cast of seed, hilar end with cast of small hilar cavity showing aperture for funicle near margin contiguous with endosperm. Fig. 21. Same, side. Cast of hilar cavity on left. Endosperm occupies lower half of figure. Chalazal region in upper half. Fig. 22. Same (hilar end only drawn), looking onto endosperm. Cast of small hilar cavity pierced by funicular aperture again seen and flanking margins of chalazal region. Chalazal region, *ch. cav*, hilar cavity (cast) with funicular aperture, *f*. *en*, endosperm ; *e*, embryo-scar.

The grounds for describing the rougher half of the seed as chalaza are the manner in which the endosperm is related to it and fused with it, the mode in which nerves on the inner margin of the endosperm are derived from it and its relationship to the hilar cavity and internal hilar scar. A chalazal region of this type is found in many palm seeds where the actual hilum is situated at one end of a large thick chalaza parallel with the longer axis of the seed and penetrating deeply into the endosperm. In such palm seeds when the chalazal tissues are removed by maceration, the endosperm shows a marked concavity where the two were fused, a few nerves may diverge from the area of fusion and the surface is fluted or slightly corrugated around the rim of the concavity. Although for the sake of clarity Palmae have been used to help elucidate and explain the structure of *Jensensispermum* no relationship to Palmae is thereby implied. In Cycads, on the contrary, the chalaza scar is simple circular and thin immediately overlying the hilum and hilar cavity.

Diameter of seeds measured at right angles to the hilar scar ; 6 to 10 mm. Maximum diameter through embryo scar and chalaza : 5 to 9 mm. Maximum diameter at right angles to the preceding : 5 to 9 mm.

REMARKS. About three hundred specimens the majority so abraded as to show

little but the internal seed-cast, with or without remains of an integument. It is always difficult to understand, interpret, and describe any specimen which has no living counterpart. The difficulties can sometimes be resolved, as in the present instance, by taking account of comparable structures in living, even if unrelated, forms. In such a comparative use of living material, it is of the utmost importance to pay due regard to the mode of preservation of the fossil so that the structures seen may be correctly interpreted, otherwise the comparison can be very misleading. In order to explain the structure of this unique plant it has been necessary to write an informal and discursive description, incorporating matter usually reserved for Remarks at the end of a more formal account. Such a departure from normal precedent was needed to justify the interpretation placed upon the organs described.



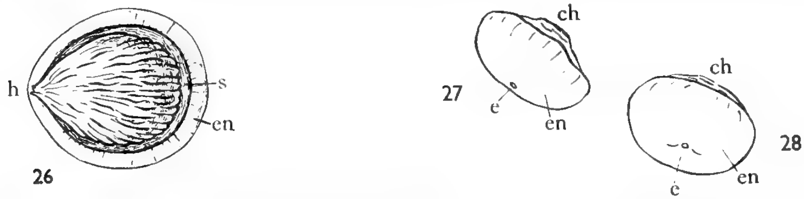
FIGS. 23–25. *Jensensispermum redmondi* gen. et sp. n. Fig. 23. Internal cast of a seed with smoothly rounded endosperm. Hilar end with concave scar which forms the inner surface of the hilar cavity. Apertures for funicular fibres are indicated. Fig. 24. Same, surface of endosperm partially embraced by edges of chalazal region. Inner surface of cavity in profile on left. Fig. 25. Same, lateral aspect with hilar scar on right. Chalazal region above; endosperm below. *ch*, chalazal region; *e*, embryo scar; *en*, endosperm; *hs*, concave scar of hilum in profile; *hf*, hilar scar (inner surface).

A proper understanding of the endosperm is fundamental to the understanding of the seeds and this has already been dealt with at some length. The significance of the hilar cavity reached on theoretical grounds is borne out by dissections of fresh seeds of *Encephalartos villosus* Lem. where a comparable shallow cavity is traversed by funicle fibres in their passage to the circular superficial thin chalaza scar at the proximal end of the endosperm. Bearing the above structures in mind the position of the hilar cavity in the fossil in relation to the rest of the seed inevitably indicates the former presence of an integument which entirely covered the whole: endosperm, chalazal region and hilar cavity. Although in many specimens it has largely disappeared its remains have been detected. The evidence of an integument which was probably pulpy and its tendency to split near the micropyle thereby producing an appearance of two "jaws" serves to connect the less abraded seeds with one almost perfect specimen (22) (Pl. 5, figs. 47–49; Text-figs. 14–16).

The systematic position of these fossils, named *Jensensispermum redmondi* for reasons given on p. 142, cannot yet be regarded as satisfactorily established. Nothing is known of the way the seeds were borne on an infructescence or axis, nor is there anything to show whether they were, or were not, enclosed in any kind of fruit or

" cupule ". While the pulpy integument, endosperm with superficial embryo-scar and hilar cavity accord with corresponding structures in Cycadales, *Jensensispermum* differs from any known Cycad in its complex chalaza, viz. the large thickened area connected at one end only with the hilum and penetrating deeply into the concavity of the endosperm. As already discussed such a structure is known to exist in Recent plants, for example in the Palmae but once again it is stressed that there is no intention of suggesting close relationship with Palms which differ in the form of the seed, absence of a large gibbous hilar scar, absence of a pulpy integument and of a comparable hilar cavity. It is suggested here that the Cycadean features may perhaps justify provisional reference to Cycadophyta pending further evidence. If this position can be entertained, the Utah seeds must belong to an entirely unknown family within that alliance.

It is possible to go one step further and to speculate whether *Jensensispermum*, with its complex chalaza unlike that of both Cycads and Gymnosperms, could be a primitive Angiosperm. But in the present state of our abysmal ignorance of what primitive Angiosperms were like, such speculation probably serves no useful purpose



FIGS. 26–28. *Jensensispermum redmondi* gen. et sp. n. Fig. 26. Seed looking onto chalazal region after abrasion of smooth layer so that the fibrous tissue diverging from hilar region, *h*, is exposed. *s*, sunk area to rear of endosperm exposed by shrinkage of chalazal region. *en*, dorsal rounded edge of endosperm seen from behind with fine fibres diverging radially from margin of chalaza. Figs. 27, 28. Detached endosperm, *en*, freed by abrasion and decay of the chalazal region, *ch*, of which slight traces only remain. *e*, embryo scar. Fig. 27. Almost true profile. Fig. 28. Tilted to show more of the outer surface of the endosperm.

although it seems right to draw attention to such a possibility. As Arnold (1959 : 7) has said of ancient fossil angiosperms " the detached condition of the organs makes it impossible to bring together enough characters for the recognition of new families ", and again, " many angiosperm families have risen and disappeared during the known course of their history just as families have in other groups, but means of recognizing them have not been devised ". It seems advisable therefore at present to resist the temptation to build an ancestral castle upon such an insufficient foundation as the imperfect knowledge at present at our disposal. We can only hope that further discoveries will reveal missing characters of this plant which will demonstrate beyond doubt its true affinities.

The fossil is depicted with the micropyle directed downwards and the chalaza occupying the upper half of the seed. This is purely a conventional arrangement pending the discovery of a sporophyll or inflorescence with seeds in the position of growth. It is quite conceivable that the micropyle was upwardly directed with the chalaza occupying the lower half of the seed.

GYMNOSPERMAE

CONIFERALES

Family TAXODINEAE

Genus *SEQUOIA* Endlicher

Sequoia sp.

(Pl. 8, figs. 75–79)

Description. The record of this genus is based on three cones which while affording evidence for generic determination are not sufficiently well preserved for specific diagnosis. All are ovoid with numerous spirally arranged peltate scales having lozenge-shaped escutcheons of which the breadth is greater than the height. The escutcheons meet edge to edge and appear to have been virtually closed when the cones were embedded. Towards the base and apex of the cones the scales diminish in size and owing to the poor preservation in these positions individual scales are there somewhat obscure. The best preserved specimen has a short stalk ; its length, including the stalk, being 23 mm. and its transverse diameters, 15 by 14 mm. Except where slight distortion has caused some confusion, the escutcheons in this specimen are clearly displayed, their maximum dimensions being 8 to 9 mm. broad and about 4·5 mm. high. Some appear to be shallow-convex superficially with an obscure transverse median ridge bearing an umbo ; others have a transverse median furrow (Pl. 8, figs, 75, 76). Traces of radial irregularities are preserved near the edges of the escutcheons indicating that the scale surfaces are reproduced in this specimen. About twenty scales can be counted on the better preserved side so that at least forty must have been borne on the entire cone.

The largest cone,about 30 mm. long, 22 by 17 mm. in maximum diameter, may have had as many as eighty scales some forty being visible on the better preserved side. Its escutcheons, 7 to 9 mm. broad, 3 to 4 mm. high at largest, are represented by light grey calcite clearly delimited by ridges of darker calcite along their margins (Pl. 8, fig. 77). Unfortunately, the surfaces representing the escutcheons show no structure or ornamentation in this specimen and appear to be purely mineral infillings of spaces formerly occupied by the distal ends of the scales. Nevertheless the specimen is of great value for it has been fractured rather irregularly not far below the middle and is about the only Utah plant yet seen which may give important information on an artificially fractured surface. The fracture must have passed in part (but only in part) along a natural plane of weakness caused by incipient separation between scales. Along this plane a thin film of calcium carbonate has infiltrated. Upon it the form and arrangement of the flattened seeds is obscurely reproduced in dark grey calcite (Pl. 8, fig. 78). This contrasts clearly with the whitish area between the seeds and the exterior of the cone representing scale surfaces. The seeds are radially arranged in relation to the cone axis, their outer ends being situated about half way between axis and external surface, their length somewhere about 4 mm. Their breadth, about 2·5 mm., when compared with that of the escutcheons suggests that at least two seeds were borne side by side on a scale but there may have been other seeds

obscured by a certain amount of overlap. The broad hilar end, by analogy with *Sequoia*, was directed towards the exterior of the cone. It may be indicated by a slight excavation on the two most distinct seeds. In one small patch near a seed margin there are impressions of rounded equiaxial pits, about 0·018 mm. in diameter comparable with the pits on seeds of living *Sequoia*. Hence there is reason to regard them as representing cells rather than crystalline structures. If so it is the only Utah plant yet seen which provides evidence of cell structure. The above interpretation is supported by the fact that the cells are much smaller than the inorganic crystalline structures which sometimes simulate cells in this material.

The third cone (V.51617) (Pl. 8, fig. 79) shows several clear escutcheons but many are obscure so that the scales cannot be counted even approximately as in the other two specimens. It is about 18 mm. long, 14 by 11 mm. broad, and is somewhat distorted obliquely.

REMARKS. The spirally arranged scales with lozenge-shaped escutcheons ornamented as described and the slender evidence as to the seeds all point to the genus *Sequoia*. *Metasequoia* and the Cupressineae are definitely excluded from relationship by the spiral arrangement of the scales in the fossil. Reference is made to the geological range of *Sequoia* on p. 141.

? Family **TAXODINEAE**

Genus ***HILLISTROBUS*** nov.

DIAGNOSIS. Small cones (?male) with spirally arranged imbricate scales narrowed at apex to form elongate tip, arising at right angles to cone axis, then bending upwards at a right angle at surface of cone. Bearing on their lower surface a number of rounded bodies (?anthers) sometimes exposed where abrasion has removed the overlapping tips of scales immediately below.

TYPE SPECIES. *Hillistrobus axelrodi* gen. et sp. n.

Hillistrobus axelrodi gen. et sp. n.

(Pls. 8, 9, figs. 80–87 ; Text-figs. 29–32)

DIAGNOSIS. That of the genus.

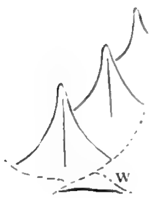
SYNTYPES. Brigham Young University, Utah, Nos. 40–42.

DESCRIPTION. *Cone.* Five small cones with uniform characters and one somewhat larger specimen (represented by the lower half only) may belong to a single species. There are also several cone fragments which are probably related. In addition a twig tip has leaves so similar in character to the lowest scales of some of the cones that it seems reasonably certain that the foliage belongs to the same plant rather than to *Sequoia* which it also somewhat resembles.

A complete ovoid cone, 12 mm. long, 7 by 8 mm. in transverse diameter is well preserved on one side (Pl. 8, fig. 80) but somewhat obscure on the other. Its thin scales are spirally arranged, overlapping with markedly acuminate tips having slightly

concave lateral margins. The extreme tips in this cone are usually broken, the scale margins are thin and delicate. They may appear irregularly and coarsely denticulate; the denticulations are probably not original but the result of a tendency of the edges to split. Each scale shows an obscure longitudinal median rib and finer longitudinal striations. At least twenty scales can be counted on the well preserved side suggesting that the complete cone must have borne about forty to fifty.

A second cone (Pl. 8, fig. 81) has similar characters but owing to crushing the scales stand out less sharply. Both surfaces of this specimen show traces of small ovoid or globular bodies, about 0·75 mm. in diameter, projecting between some of the scales. It is not clear in this specimen whether they have a structural significance or are due



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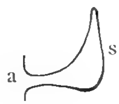

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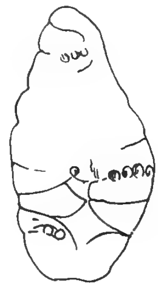

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Figs. 29–32. *Hillistrobus axelrodi* gen. et sp. n. Fig. 29. Diagram to show parts of cone scales exposed at surface of cone with acuminate tips, slightly concave margins and slight median longitudinal angles. Dotted lines indicate where overlapping scales below are broken. *w*, worn stump of a cone-scale which has lost its elongate tip by abrasion. Fig. 30. Diagram based on part of a transversely fractured cone where thickness and overlap of scales are partly shown in section. Fig. 31. Diagram to show how, seen in longitudinal section, the scale arises at right angles to axis, *a*, at centre of cone; then takes a sharp right angled bend upward at surface of cone, *s*. At the upward bend there is a thickening to close gap between it and scales below. Fig. 32. Rough diagrammatic sketch based on specimen 47 to show rounded bodies (? anthers) fringing worn edges of some scales.

to some peculiarity of preservation. The number of scales cannot be counted. Length of cone, 17 mm.; diameter, 11·5 by 9·5 mm.

A third cone is the lower two-thirds (approximately) of a more elongate specimen. It shows clearly the attenuated form of the scales and some of the scale tips are perfect (Pl. 8, fig. 85). The basal scales are small and the two lowest may possibly be foliage leaves. They are opposite and seem to link this species with the foliage mentioned above. Above this pair of (?) leaves the scales are spirally arranged as in other specimens. The cone is fractured transversely above but unfortunately the section shows no structure. Length of cone as preserved, 14 mm.; diameter, 9 mm. The appearance of this specimen and the absence of any clear footstalk suggest that the cone was not sharply delimited from the foliage but gradually merged into it.

The cone depicted in Pl. 8, figs. 82, 83 although the upper half only of a small ovoid specimen displays very clearly the spirally arranged scales with well preserved

complete tips. The scales become very small at the apex of the cone. One surface has suffered much abrasion which has removed the thin pointed tips leaving only the worn rounded stumps of the thick middle part of the scales. On the worn surface one or two subglobular bodies are again seen between the scales and on the transversely fractured surface which forms the base of the specimen they are also present but their arrangement is obscure. The fractured surface indicates that the scales arise at right angles to the cone axis and only at the circumference of the cone do they bend upwards at a right angle to form the overlapping subtriangular pointed scale tips described (Text-fig. 31). The lower edge of the scales at the circumference appears to be slightly thickened so as to meet in close contact the surface of scales immediately below. Maximum length represented, 10 mm.; diameter, 9 mm.

A fifth cone (46) is a mere fragment. The apex and half the surface have gone and the base is slightly incomplete. Unfortunately the oblique-longitudinal section shows no structure. There is one pointed scale with tip preserved, and another much worn and therefore rounded. The obscure rounded bodies are seen on the worn surface and may be exposed by abrasion of scales which overlay them. Length of fragment, 14 mm. ; breadth, 9 mm. ; thickness from exterior to sectioned surface, 5·5 mm.

Another cone (44) is very obscure and is obviously the lower half of a larger one about 15 mm. in diameter. 11 mm. of the cone length are preserved. Unlike all other specimens there is a short footstalk but the details of scales are obscure at the surface which is much corroded. The basal scales correspond in character with those of specimen (41). Irregular rounded projections here appear to have no significance structurally. The transverse fracture does nevertheless show, in places, the thin scales, in section, overlapping others with concave upper and angled lower surface and attenuated margins (Pl. 9, fig. 87 ; Text-fig. 30).

The cone (47) is much distorted, abraded and imperfect but it shows definite rounded bodies fringing the worn edges of some of the scales (Text-fig. 32). Other specimens are too broken to merit individual description and make no special contribution to the elucidation of this species.

Foliage. (Pl. 8, fig. 86). A small twig tip, 13 mm. long, incomplete at the extreme apex which may have borne either a cone or a foliage bud. It is 6·5 by 5 mm. in maximum diameter, differences of breadth which may be due to a slightly bifacial form. The small spirally arranged leaves are imbricate, scale-like, closely investing the stem, angled medianly on the lower side especially at the sides of the twig in the broader plane. There is no evidence of cell structure. All or part of twelve or thirteen leaves can be counted on the broader surface. The longest marginal leaf is about 6·5 mm., its breadth from margin to midrib about 2·5 mm. The longest leaf seen on the broader surface is about 6 mm. and its total breadth from margin to margin, 3·25 mm.

A larger twig fragment, 26 mm. long, 8 by 10 mm. broad shows lozenge-shaped leaf scars but is in poor condition. The scars and outer tissues of the twig are worn away at one end exposing a woody axis with no structure preserved. This fragment may belong either here or with *Sequoia*.

REMARKS. Once again the interpretation of this species is difficult because of the crystalline character of the casts by which it is represented. Specimens were shown to Prof. T. M. Harris but were unknown to him. He drew attention to their superficial resemblance to *Sphenolepis* Schenk from the Wealden of Belgium (Harris 1953 : 5) represented by foliage and female cones but the specific limits of *Sphenolepis Kurriana* (Dunker) are, he pointed out, ill-defined. The scales of the Utah cones are certainly more markedly attenuated. Nor is the resemblance to the Wealden genus *Elatides* Heer (see Harris 1953 : 21) any closer. Whether a ligule is present or not on the upper surface of the scales cannot be ascertained. If these cones are female structures they certainly differ markedly in their thin overlapping scales with long narrow tips and lack of any definite ornamental escutcheon (Text-fig. 29) from *Sequoia* (p. 157). The presence of the small ovoid or rounded bodies described above, especially when these appear to project from the lower side of the scale, raises the question whether the cones could be male organs and the rounded bodies anthers. There is nothing in the form of cone or scale to preclude this possibility. Whereas many coniferous male cones are very small, some, those of *Araucaria* for instance, may be larger than the fossil cones. Traces of the " anthers " are visible both in specimens with abraded rounded scales and in those which still carry the unworn attenuated tips. They may however be a result of partial decay and abrasion and not definite organs. In spite of the many gaps in our knowledge of this species it seems to have readily recognizable characters. In order, therefore, that it may be kept in mind in future investigations, it has been called *Hillistrobus axelrodi*. The reason for this name is explained on p. 141.

A number of syntypes have been selected so as to demonstrate as far as possible the characters of scales and cones.

Genera ?

(Pl. 9, figs. 88, 89)

A cone 19 mm. long, 15 mm. in transverse diameter, without foot-stalk, having spirally arranged scales (Pl. 9, fig. 88). Three small scales at the extreme base are thin especially at the margins and narrowed to a point at their distal extremities. Scales over the main body of the cone appear to have suffered much abrasion which has removed their thin imbricate distal ends (if they ever existed) leaving the thickened rounded, smooth middle part of the scale projecting (cf. the abraded side of *Hillistrobus* cone Pl. 9, fig. 83 which they resemble but on a larger scale). These worn scales, almost as broad as the cone itself and about 4 mm. high, are difficult to count. About fifteen are visible on one surface suggesting at least thirty on the whole cone, a smaller number than that on the male(?) cones of *Hillistrobus*. Above the scales in some instances is a low triangular flattened area, possibly the part impression of the former distal prolongation of a subjacent scale on a film of calcite between it and the scales above. The form of the triangle suggests that the prolongation, if it existed, must have been shorter than in *Hillistrobus*. It is permissible to speculate whether this larger cone could be a female example of that genus in a somewhat

abraded condition, but there is no evidence to confirm or refute this suggestion. It can be stated confidently that the *Sequoia* cones described on p. 157, even abraded, would be unlikely to produce the appearance here shown. In fact there are no grounds for regarding this cone as ever having had scales with escutcheons meeting edge to edge as in *Sequoia*.

A red siliceous cast (Pl. 9, fig. 89) 22 mm. long as preserved (imperfect at the tip), 15 mm. in transverse diameter is too ill-preserved for speculation as to its relationships. The scales are small, spirally arranged, overlapping, sharply pointed above, with very slightly concave margins flanking the point and a slightly convex outline below the broadest part exposed at the surface. Maximum length of scale exposed, 3 mm.; maximum breadth, 4 mm.

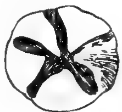
INCERTAE SEDIS

Genus ***CARPOLITHUS*** Linnaeus

Carpolithus provoensis sp.n.

(Pl. 9, figs. 90–92; Text-figs. 33–36)

DIAGNOSIS. Integument or cupule rounded-obconical elongate, lobes free only at flattened apex where there are five ? pointed unequal segments. Base with two short unequal facets inclined at an angle of 90° and, on opposite side, a short deep cleft. Surface irregularly longitudinally furrowed, many furrows short and discontinuous.



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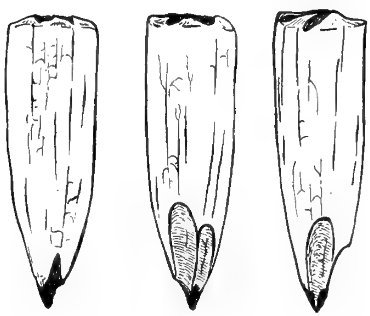

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FIGS. 33–36. *Carpolithus provoensis* sp. n. Fig. 33. Apex with appearance of sepals, four of which are clearly seen and a fifth, partly visible is indicated also by the spacing. Fig. 34. Side, showing deep basal cleft or furrow and flattened apex. Fig. 35. Opposite side, showing two unequal basal facets. Fig. 36. Side at right angles to fig. 35. One facet here appearing as a basal excavation, the other facing the observer.

Transverse nervules divide surface into rectangular areas. Length, 26 mm.; apical diameter, 11 by 9 mm.

HOLOTYPE. Brigham Young University, Utah. No. 50.

DESCRIPTION. Seed enclosed in an integument or cupule which is rounded-obconical and elongate, its lobes united except at the flattened apex. Base more or less pointed with a short deep cleft or furrow (about 4 mm. long) on one side (Pl. 9, fig. 91; Text-fig. 34) and two unequal facets, inclined to one another at an angle of about 90° on the opposite side (Pl. 9, fig. 90; Text-fig. 35). One facet is 10 mm. long with maximum breadth of 4 mm.; the other is 7 mm. long with maximum breadth about 3 mm. The furrow and facets could be caused by pressure from a stem and adjacent seeds. The whole surface is irregularly longitudinally furrowed, many of the furrows being short and discontinuous, others longer, none extending throughout the length. Remains of transverse nerves are also seen which appear to divide the surface into small rectangular areas. There may be slight indications of branching and anastomozing of nerves. In places the surface appears finely longitudinally striate and perhaps formed of small equiaxial rounded cells about 0·038 mm. in diameter, but these are obscure. Cell structure and furrows are continued onto the facets suggesting these are due to secondary pressure. Apex partially hidden by five ? sepal-like pointed segments of the integument which bend over it crossing the apical margin at a sharp angle. Segments not all equal in size, extending almost to the centre of the apex, partially obscured by adherent matrix (Text-fig. 33). Length of integument, 26 mm. Diameter at apex, 11 by 9 mm.

DISCUSSION. Nothing is known of the interior of this specimen but it may be supposed to enclose a seed. Relationship to Pteridospermae is not excluded by the superficial features which are the sole available evidence. Andrews (1963, text-figs. 4–9) illustrates a number of Pteridosperm seeds covered by integuments showing considerable variation in the degree of fusion of the lobes. In his text-fig. 18 Andrews illustrates a *Lyginopteris* seed with apex having the same form as the fossil but otherwise unlike it. Since this one much younger specimen only yields such limited information nothing definite can be said as to affinities The specimen is referred to the form-genus *Carpolithus* as *C. provoensis* sp. n.

Carpolithus radiatus sp. n.

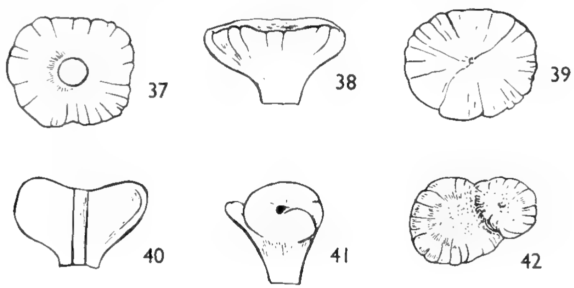
(Pls. 9, 10, figs. 93–130; Text-figs. 37–42)

DIAGNOSIS. Stalked circular peltate seeds about 8 to 15 mm. in diameter with thick integuments enclosing in some cases cast of seed cavity of albuminous seed. Seed casts compressed at right angles to axis sometimes having a central depression connected with the margin on one side by a radial channel. Micropyle central ? Chalaza on lower surface contiguous with stalk. Hilar scar marginal indicated by truncation on cast. Few specimens showing narrow radial cavities instead of seed-casts (? anthers). Some of these have a stout central canal with fibre strands extending throughout their length.

SYNTYPES. Brigham Young University, Utah, Nos. 51, 53, 58–60.

DESCRIPTION. A plant, represented by over thirty specimens, difficult to describe because not fully understood. This is partly due to the great limitations of this type of preservation, partly to the incomplete, fragmentary character of the material, and partly to the fact that nothing comparable, either living or fossil is known. The specimens show variations of form within certain limits and differing degrees of abrasion. From a few which display something of the internal structure two distinct organs are probably represented but from the external characters alone it is not always easy to discriminate infallibly between them. In general all are peltate with thick central stalk, broken off shortly, which widens upwards at first gradually, then suddenly to produce a subcircular apical disc of varying thickness (Pl. 9, figs. 93–100; Text-figs. 37–39). The lower surface of the disc is obconical or convex (51, V.51619; Pl. 9, figs. 94, 95, 100, 101; Text-figs. 38, 41), the upper surface may be shallow obconical or concave (51, 55), flat (52) or slightly convex (58; Pls. 9, 10, figs. 93, 96, 117, 119). The lateral margin of the disc may be sharp (? if worn) but is more often rounded and inflated in varying degree (52, 54, V.51621, V.51622; Pls. 9, 10, figs. 97, 109). A few specimens exhibit marked dorsiventral inflation (54, V.51622; Pl. 10, figs. 113, 115). In almost all cases both surfaces show radial furrows occupied by fibres traceable either for short, variable distances or from the margin to the centre. In general these fibres diverge from the stalk below (or from its direction) and converge towards the centre of the disc above so producing an irregularly fluted margin. One specimen (58) is partly covered by an outer (?) epidermal, layer preserved only on the upper surface. It is rugose and has a central mucro (Pl. 10, fig. 119), a somewhat similar mucro is seen in (60) (Pl. 10, fig. 127). This latter had been fractured in a median longitudinal plane before fossilization and shows a central fibrous axis terminating above in the mucro (Pl. 10, fig. 128). Two other longitudinally fractured specimens (57, V.51623; Pl. 10, figs. 124, 126) show the central axis as a hollow canal. V. 51623 and 60 appear to have narrow radial cavities flanking the axis (Text-fig. 40) while in (57) there may be an obscure cast of such a cavity. One specimen (62) has superficial rugosities corresponding in direction to the furrows and alternating ridges described above. These could indicate a pulpy layer now dried and partly shredded, commonly wholly abraded. The stalk of this specimen, also of (56), displays in cross section a central cavity and coarse radial structure emphasized by a tendency to crack (Pl. 10, fig. 118). One club-shaped specimen (61) with ellipsoid head instead of a dorsiventrally compressed disc has similar fibres converging to the apex (Pl. 10, figs. 129, 130). In spite of its different shape it is so closely comparable with the others in its surface that it is regarded provisionally as belonging to the same species. It may represent an immature seed or a barren shoot tip. The other differences alluded to whether in degree of inflation or in form would all probably have been attributed to different stages of development but for the few imperfect or abraded specimens which indicate that true internal structural differences exist. A few of the more inflated examples show the internal cast of an albuminous seed, the seed having been exposed before fossilization by decay or abrasion of its integuments which form the disc. Such

casts which are only slightly dorsiventrally compressed have an inflated rounded margin (53, V.51620, V.51622). All show a marked central depression which may be continued to the margin along one radius as a channel. Thereby the effect of a curved seed cavity is produced (Pls. 9, 10, figs. 102, 105). A small twig embedded in the endosperm of (54) suggests that this tissue in life was fairly soft. Clearly such well filled seed-bearing specimens are of different structure and significance from those referred to above with flattened radial cavities. The true nature of the latter cannot be established on the evidence of available material but they could be male organs or barren shoots with internal floats. The former seems to be the more probable hypothesis. Unisexual organs are common in Mesozoic vegetation. A few of the inflated specimens (especially 58 but the evidence is also seen in 63, V.51622, V.51625)



FIGS. 37–42. *Carpolithus radiatus* sp. n. Fig. 37. Base of a seed showing central stalk and radial marginal furrows. Fig. 38. Side, showing slight concavity of apex, sometimes present, and rounded margin. Fig. 39. Apex, radial furrows again shown diverging from central micropyle (?). Fig. 40. Median longitudinally sectioned specimen with central longitudinal canal and fibres and shallow radial cavity on right. Fig. 41. Apicolateral view of seed with internal cast (= endosperm) exposed by abrasion of integument. Central depression and embryo scar and channel between the latter and the margin are seen. On left is a second young seed (or ? shoot in early stages). Fig. 42. Apex of two contiguous seeds growing, almost fused, on the same stalk. Stippling indicates adherent matrix on their surfaces.

have lost the stalk and lower part of the integument, presumably destroyed before fossilization. In such instances a transversely rugose lower surface of the seed cast is exposed (Pl. 10, fig. 120). It recalls the tissues of the chalazal region in *Jensensispermum* (p. 156) but in the present instance the region is situated on the lower surface of the seed above the erect stalk (raising the question whether the chalaza in *Jensensispermum* should be placed below rather than above). The rugosities tend to diverge from a point near the circumference. In 63, V.51625 there is a marginal truncation at this point, emphasized by a raised rim. In 58 scar and rim are not clearly defined but the rugosities with marginal divergence are particularly clear (Pl. 10, fig. 120) as is the radial arrangement of the upper surface (Pl. 10, fig. 119). It seems probable that the point of divergence and truncation indicate the hilar scar at one side of the chalazal region as in *Jensensispermum*. The specimen which best shows the curved appearance and apical depression of the endosperm (53) also dis-

plays a small bud-like projection arising on the stalk at the opposite end of the diameter through the radial channel in the endosperm (Pl. 10, figs. 105, 106; Text-fig. 41). This may indicate the beginnings of a second seed or shoot (cf. also V.51626). That duplication of organs does occur is clearly visible in 59 (Pl. 10, figs. 121, 122) where two contiguous seeds on the same fused stalk are so closely adpressed as to cause deformation of the larger one (Text-fig. 42). Except when seed casts or radial cavities are well developed or exposed by abrasion or fracture it is not always possible to be sure whether a given entity is (?) male or female (i.e. assuming that the specimens with radial hollows are, in fact, correctly interpreted as male organs).

The diameter across the apical disc varies from about 8 by 8 mm. to 15 by 11 mm. Frequently there is a maximum diameter while that at right angles to it is shorter. The diameter across seed-casts seen is 8 by 8 mm. to 11 by 12 mm. and 13 by 10 mm., and the dorsiventral thickness, 8 to 10 mm. The maximum length seen from the top of the apical disc to the lower end of the broken stalk is 10, 9 and 12 mm. The mode of growth of this plant is unknown and it is impossible on the present limited evidence to make any suggestion as to its systematic position. It may well represent an extinct phyllum. While awaiting better information the species is described and figured as *Carpolithus radiatus*.

The temptation to regard it as a pedunculate fruit enclosing a seed has been resisted on account of the features which these seeds have in common with *Jensensispermum redmondi*: viz. the albuminous character and the relative positions of chalaza, hilum and micropyle in relation to the endosperm. Indeed the seed cast resembles a rather compressed seed of *Jensensispermum*. The similarity suggests kinship between the two but consistent compression and the radially ornamented and expanded integument around the flattened seed indicates that they must be distinct genera even if related.

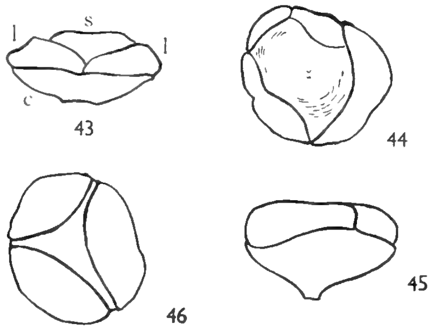
Carpolithus sp.

(Pl. 11, figs. 131–134; Text-figs. 43–46)

The appearance of two subglobular but somewhat crushed specimens is that of a "berry" partially enclosed in a cupule which is lobed above. The first (Pl. 11, figs. 131, 132; Text-figs. 43, 44) has been much compressed dorsiventrally so that it is now only about 9 mm. long but 26 mm. in transverse diameter. Its surface is abraded and rugose. No cell structure or tissues of any kind can be detected. The entity enclosed which could well be a seed is exposed naturally at the apex of the gaping cupule and, by abrasion, at the base also where cupule and attachment have been worn away (Pl. 11, fig. 132). At the equator a horizontal furrow may have structural significance but it may perhaps have been deepened as a consequence of crushing. Below the furrow the cupule is fused (Text-fig. 43). Above it is divided into four distinct low rounded lobes which extend up the sides for perhaps two-thirds of its original length. The lobes are unequal (Text-fig. 44). Two adjacent larger lobes occupy about two-thirds of the circumference while two smaller ones

together occupy the remaining third (Pl. 11, fig. 131). One of the smaller lobes appears to overlap the smaller and larger lobes adjoining it. The second smaller lobe is overlapped by the second larger lobe. The two large lobes are barely contiguous at their junction.

The second specimen, although also much abraded is relatively unworn and uncrushed below but flattened and compressed above. It shows remains of a prominent pointed attachment situated medianly on its broadly obconical lower surface (Pl. 11, fig. 134; Text-fig. 45). The demarcation between the fused lower and lobed upper parts of the cupule is made more obvious by a difference in the colour of the cast. The lower part is of grey calcite and the upper of red. There are only three lobes, approximately equal in breadth, without evidence of mutual overlap.



FIGS. 43–46. *Carpolithus* sp. Fig. 43. Side view of dorsiventrally compressed seed, *s*, in cupule, *c*, with separate lobes, *l*, above the equator. Fig. 44. Same, apex, showing four unequal lobes surrounding and partially concealing the seed. Fig. 45. Another specimen, side, with entire cupule on lower part, lobed segments above. Fig. 46. Same, apex, showing the three lobes largely overlapping and obscuring the much flattened seed.

The upper limits of one lobe are a little obscure (Pl. 11, fig. 133; Text-fig. 46). Diameter of this specimen, 27 by 21 mm. Length including attachment, 25 mm.

The true nature of the object within the cupule can only be guessed in the absence of evidence as to its structure or integuments but it could be a seed of Pteridospermous type. In the circumstances it is impossible to do more than describe the two specimens as *Carpolithus* sp.

A number of isolated, irregular, featureless, subglobular bodies also occur in the deposit. While they have the appearance of tubers, they could equally well be ill preserved seeds, like those in the cupules described above or fungi or algae. They are of comparable size but appear to lack any distinctive features apart from several obscure circular depressions filled with matrix which may or may not be of any significance. One or two of these organs are shown in Pl. 12, figs. 148, 149 (cf. also V.51813–14).

Carpolithus sp.

(Pl. 11, figs. 135–145)

About a dozen specimens, almost all of which are considerably broken, show certain features in common. They are more or less fusiform and longitudinally striate. Some of the striae are deep and well marked and may extend throughout the length preserved. Others are shallower and impersistent. One (Pl. 11, figs. 135, 136), pointed at one end, truncate through a break at the other, shows close-set finer sinuous furrows and ridges between the deeper conspicuous ones. There seems to be a tendency for these objects to split longitudinally along the more conspicuous and persistent grooves, but there is no evidence of splitting into a definite number of segments. A possible alternative interpretation is that these bodies are formed by the partial fusion of separate segments. One (Pl. 11, fig. 145) is pointed at both ends. Another (Pl. 11, figs. 143, 144) is pointed at the perfect end but broken at the other. While (V.51628; Pl. 11, figs. 137, 138) appears to have been pointed at both ends although both are very slightly imperfect. Two specimens are peculiar in having at one extremity an expanded disc-like region (Pl. 11, figs. 139–142) separated by a narrow neck from the main area. This could be a crushed cupule but has the appearance of a sucker-like attachment. The preservation is too obscure for its true nature to be ascertained. In both the disc is bent, possibly secondarily but prior to fossilization, almost into the plane of the major part described above. Some at least of the furrows extend onto the disc. A smaller object, (74) embedded in matrix (only about 13 mm. by 7 mm., slightly imperfect at one end) shows as an impression in the matrix what may be also the impression of a small cupule. It is not clear whether this should be grouped with the above.

Unfortunately none of these specimens, even when broken and imperfect shows any shred of evidence as to structure or organs within. There are therefore no grounds for suggesting that a seed is enclosed by a ridged and furrowed integument. It is impossible, in the circumstances, to form any opinion as to their nature, but their relationship may at some future time be determined if better preserved material showing these characteristics is found. Consequently, it seems worthwhile to illustrate them and to publish this brief account.

(Pl. 11, figs. 141, 142)

Dimensions of specimens: (70) Length, including disc, 38 mm. Breadth (as crushed), 23 by 10 mm. Breadth across constriction which delimits disc, 18 mm. Length of body above disc, 29 and 25 mm. respectively on opposite sides.

(Pl. 11, figs. 143, 144)

(71) Organ with no disc preserved. Length, 40 mm. Breadth (as flattened), 21 by 10 mm. The "segments" in this specimen appear to be somewhat obscured by matrix which may, or may not, represent an outer layer of integument.

(Pl. 11, figs. 135, 136)

(68) Length broken at one end (no disc) about 23 mm. Breadth, 15 by 6 mm.

(Pl. 11, figs. 137, 138)

(V.51628) More slender, perhaps immature, slightly imperfect at both ends. Length, 26 mm. Breadth, 12 by 5 mm.

(Pl. 11, fig. 145)

(72) One side much obscured by adherent matrix the other partly obscured. Both ends more or less complete but no " disc " preserved. This fact suggests that the " disc " is a cupule if the specimen is really related to the others. Length, 30 mm. Breadth, 18 by 12 mm.

(Pl. 11, figs. 139, 140)

(69) Smaller with well marked " disc " and almost perfect apex. Length, 25 mm. Breadth, 11 by 9 mm. Breadth of neck, 10 mm. Breadth of disc, 14 mm.

In addition some broken or imperfect specimens not figured and two (V.51629) in the British Museum (Natural History). All others Brigham Young University, Utah.

Unknown Organisms

(Pl. 11, fig. 146 ; Pl. 12, figs. 147, 150–154, 156, 158)

A large subcircular body, now much flattened apparently dorsiventrally. An irregular pitted central prominence on one side (Pl. 12, fig. 150) suggests an attachment. Beyond this central region fine concentric striations or wrinkles are visible. On the opposite broad surface similar features are seen (Pl. 12, fig. 151, cf. also V.51807–08, V.51811–12). The nature of these bodies is obscure. Diameter of figured specimen 40 by 36 mm. ; height, 16 mm. A second imperfect specimen, broken so as to display a longitudinal section shows a central cavity now wholly occupied by quartz crystals (Pl. 12, fig. 152). The significance of the superficial concentric structure is not clear. It suggests a mode of growth emphasized and made conspicuous by contraction on drying.

Numerous similar cake-like organisms show in varying degree a tendency to disintegrate radially and/or concentrically. Some are larger, others smaller than the specimens described above. While they bear a superficial resemblance to some fungal fruiting bodies they show no clearly defined diagnostic character on which a satisfactory determination can be based (see p. 143).

In some cases these bodies are twinned (Pl. 12, fig. 147) two growing in close contiguity causing mutual flattening along the contiguous surfaces. The figured specimen is 30 by 25 mm. in diameter, the individuals of the pair being about 17 and 12 mm. in maximum diameter respectively. Some apertures on the surface could be due to crystalline inorganic structures. There is no definite evidence for interpreting them as perithecia.

Pl. 12, fig. 156 is a distorted subglobular body, 18 by 16 mm. in diameter, which has started to split into petal-like segments. It has a peculiar irregularly cracked and

fissured surface. The superficial appearance suggests fungus but satisfactory evidence of its nature is again lacking.

The object in Pl. 12, figs. 153, 154 has a curved obconical form with shallow convex upper surface. Only half of the original appears to have been preserved it having split longitudinally through the curved pointed end and along the broadest diameter of the convex surface prior to fossilization. It has a fibrous appearance, the "fibres" diverging from the pointed end and branching repeatedly. Where they impinge on the convex surface they produce a radial structure. Whether they are true fibres or of chemical origin seems doubtful. There seems to be a tendency to shred and weather along the lines they produce. One margin of the fragment from the point to the edge of the convex surface is 30 mm. long, the other 20 mm. The thickness from the margin of the rounded outer surface to the plane of fracture is 15 mm. The maximum diameter of the convex surface is 39 mm. There is no evidence of an outer integument but the roughness of the surface preserved suggests that if the body is of organic origin such an integument would formerly have covered it. No suggestion as to the nature of this specimen can be made. The fact that it might show the internal structure of bodies like that in Pl. 12, figs. 150, 151, pure moulds of hollow casts of former entities, should be remembered (cf. V.51804, V.51815).

It is quite impossible either to describe or figure the innumerable tuber, alga, or fungus-like bodies which occur in this deposit. They show great variety of form and size. Two final examples have been selected for illustration because they bear a purely superficial and misleading resemblance to pods of higher plants. One is elongate with a narrow rim, and is incomplete at each end. It is 35 mm. long, 14 mm. broad, 4 mm. thick (Pl. 11, fig. 146). The other is flattened and subcircular, 21 by 23 mm. in diameter, also with an obscure rim (Pl. 12, fig. 157). In both the surface is irregularly pitted and around the edge cracked and fissured. No explanation of these curious bodies can be offered.

Thorn

(Pl. 12, fig. 155)

A large detached thorn, down curved as seen in lateral profile so that its outline above is slightly convex and below slightly concave. The base is broad, subelliptical, with a somewhat convex surface which lies oblique to the thorn itself which is therefore asymmetric on the two sides. The more convex side carries a median rounded angle throughout its length. The base measures 28 mm. longitudinally by 18 mm. transversely. A straight line drawn from the upper edge of the base to the tip of the thorn measures 28 mm. and from the lower edge to the tip only 21 mm. A smooth surface is preserved all over the longer more convex side but only at the proximal end of the shorter side. Here it is abraded towards the tip exposing a coarsely fibrous structure. As there is nothing to connect the specimen with any other plant remains its systematic position cannot be determined and no name can be given.

POSTSCRIPT

After this MS. was completed a periodical reached the British Museum (Natural History) in December 1964 which included a brief note on some similar fruiting organs and one or two additional ones from the northern Henry Mountains (flanks of Mt. Ellen) in south-eastern Utah. They were apparently derived from the Morrison bedrock at the collecting site. The author of the note, Charles Bass (1964 : 94, 95 ; two half-tone figures in text each showing a number of the specimens) states that they are suggestive of both angiosperm and gymnosperm fructifications although no formal identifications had been made. His MS., accepted on 25th April, 1964, was published in July 1964. Among specimens figured are *Behuninia*, *Jensensispermum* and *Carpolithus radiatus* all described in the foregoing pages in which the present writer's views on the affinity of these forms is clearly stated.

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EXPLANATION OF PLATES

Transverse striations in the plates are due to faulty technique in collotyping and are not structures present in the fossils or faults in the original photographs.

All specimens are from the Morrison Formation, Utah. See p. 139.

PLATE 1

Behuninia joannei gen. et sp. n.

FIG. 1. Syntype. Detached distal end of a sporophyll, upper side, incurved over two young seeds. Left side incomplete as indicated by broken line. Cut lower end of fragment at *s*. Dissected free ends at *t*. ×6. (1.)

FIG. 2. Same, lower side. Axis, *a*, between young seeds shows longitudinal nerves connected by slender transverse branches. ×6.

FIG. 3. Syntype. A young terminal seed, lower side, attached to rachis, *r*. Attachment facet in lower half of figure. ×6. (2.)

FIGS. 4, 5. Syntype. Two opposite obovoid seeds still attached to rachis. *r*. Longitudinal nerves are seen on the rachis and converging to the apices of the seeds. Fig. 4, upper side; fig. 5, lower side. ×3. (4.)

FIG. 6. Seed in fig. 3, upper surface. ×3.

FIG. 7. A young seed near distal end of sporophyll still attached to rachis. A second sub-opposite seed, borne at *s2*, is not preserved. ×3. (3.)


r
r
5
4
r
r
a
6
S2
2
7
a
t
t
r
3
s
1

PLATE 2

Behuninia joannei gen. et sp. n.

FIG. 8. Pair of small subglobular distal seeds still attached. ×3. (V.51588.)

FIG. 9. Pair of rounded seeds, *s*, attached to rachis, *r*, lower side. Endosperm of seeds exposed. ×2. (V.51589.)

FIG. 10. Same, upper side, showing closer approximation of seeds. Lettering as in fig. 9. ×2.

FIG. 11. Syntype. Pair of seeds, *s*, attached to broad rachis, *r*, lower side. Embryo vesicle at *v*. ×3. (8.)

FIG. 12. Same, viewed from distal end. Embryo vesicle, *v*, preserved in grey matrix shows clearly in actual specimen, against pink endosperm. ×3.

FIG. 13. Pair of abraded seeds still attached. Terminal embryo vesicle depression at *v*. *r*, rachis. *vl*, ?lateral embryo vesicle. ×2 approx. (V.51594.)

FIGS. 14, 15. Syntype. Pair of larger ovoid seeds (one imperfect) attached to rachis, *r*. Terminal embryo vesicle at *v*. Fig. 14, lower surface, fig. 15, upper surface. In fig. 15 worn remains of longitudinal fibres are seen on left seed converging towards the terminal embryo vesicle. ×2. (5.)

FIG. 16. Two unequally developed attached seeds, lower surface, showing discontinuous branched nervation. ×3·3. (V.51590.)

FIGS. 17–19. Syntype. Somewhat abraded seed with dried pulp exposed forming irregular ridges which converge to the apical embryo vesicle. Lateral vesicle (?abortive) seen as circular scar from which furrow, *f*, runs to base separating a snout-like region, *sn*, from the rest of the seed, Basal area smooth because still retaining outer layers elsewhere abraded. (9.) Fig. 17, side × 2·5. Fig. 18, side × 6·5. Fig. 19, apex showing converging rugosities of dried pulp ×2·5.

FIG. 20. Syntype. Rounded well-developed seed broken from axis. Apical embryo vesicle at *v*. Remains of striate fibrous integument or bract below with broken edge at *b*. ×2·2. (7.)

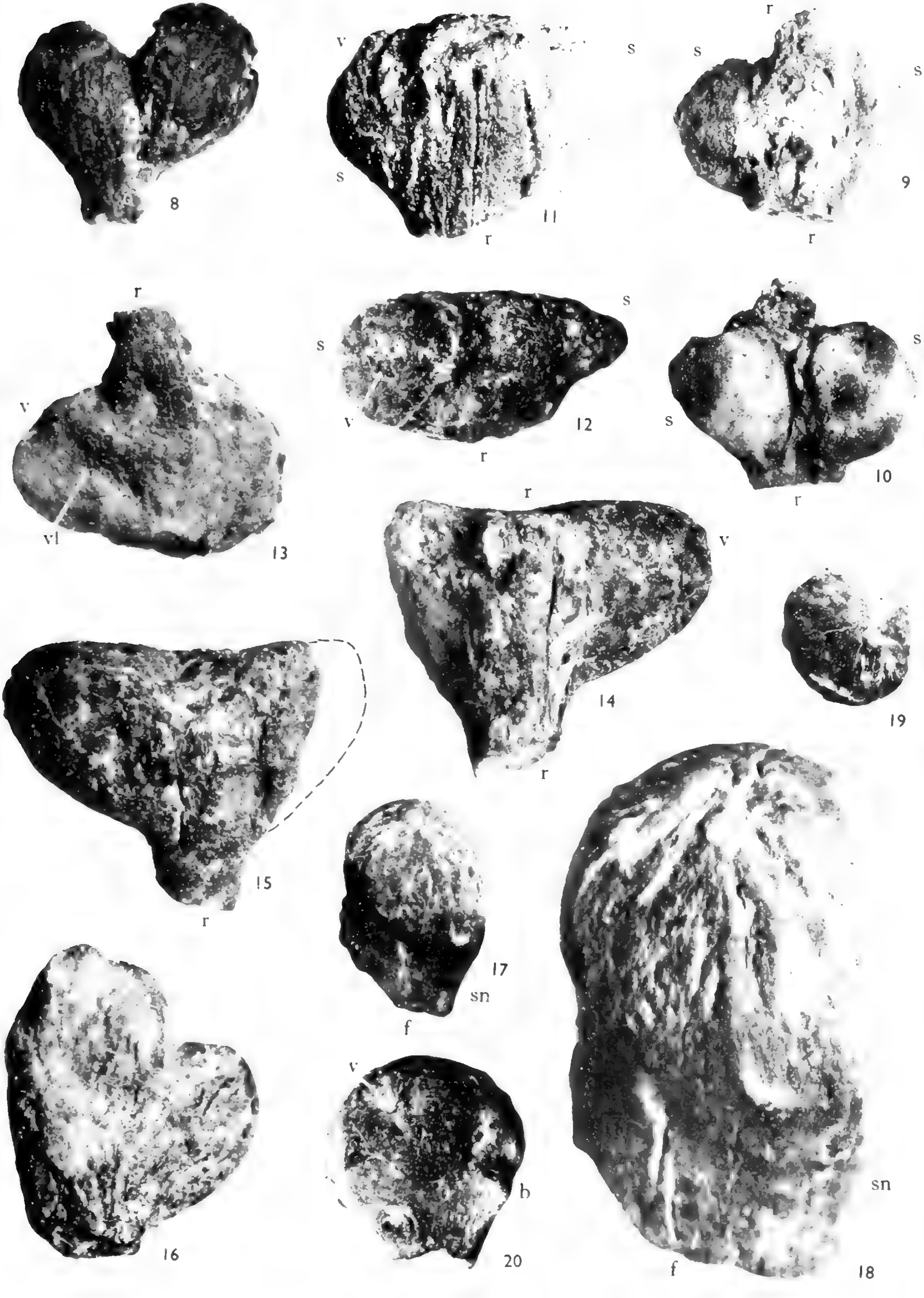
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PLATE 3

Behuninia joannei gen. et sp. n.

FIG. 21. Syntype. Seed, apex, with hard integument exposed by abrasion showing apical vesicle (white circular scar) and simple longitudinal fibres diverging from it. ×2·5. (10.)

FIG. 22. Same, attachment side showing facet, *f*, below, and longitudinal fibres diverging from apical vesicle to margin of facet. ×2·5.

FIG. 23. Seed cast representing endosperm; terminal embryo vesicle at *a*. Lateral vesicle light coloured depression. Longitudinal furrow from the latter separates snout, *sn*, from rest of seed. Base broken. ×2·2. (V.51593.)

FIG. 24. Same, apex. Terminal vesicle seen as light coloured patch and attachment facet, *f*, forms a low projection in profile. ×2·2.

FIG. 25. Detached seed. Attachment side; *f*, attachment facet. Branching fibres of surface well preserved. *sn*, snout. × 3 approx. (20.)

FIG. 26. Same, opposite side with well preserved rugose external surface. Snout-like region on right. × 3 approx.

FIG. 27. Much corroded seed with dried pulpy layer exposed. Still attached to fragment of sporophyll, *sp*. The snout-like region (split longitudinally) faces the observer. ×3. (V.51592.)

FIG. 28. Same, viewed at right angles to preceding with snout, *s*, to left, remains of rachis (sporophyll) *sp*., to right. ×3.

FIG. 29. Detached somewhat crushed larger seed, probably this species. ×3 approx. (16.)

FIG. 30. Pyriform smooth detached seed, attachment side. Split at apex indicates micropyle and embryo vesicle. ×2·2. (17.)

FIG. 31. Apex of the same, showing split. ×2·2.

FIG. 32. Another inflated smoothly rounded seed. *v*, apical vesicle slightly asymmetrically placed. ×2·2. (18.)

FIG. 33. Apex of same showing two small apertures closely adjacent (?twinned vesicles). ×2·2.

FIG. 34. Small pointed seed with remains of outer integument. Shows lateral vesicle as circular scar, *v*, connected with base by a furrow (incipient split) which separates the snout, *sn*, from the main body of the seed. ×6·5. (V.51591.)

FIG. 35. Same, opposite side, showing large attachment facet, *f*, occupying more than half the length adhering to a fragment of longitudinally striate rachis on right. ×6·5.

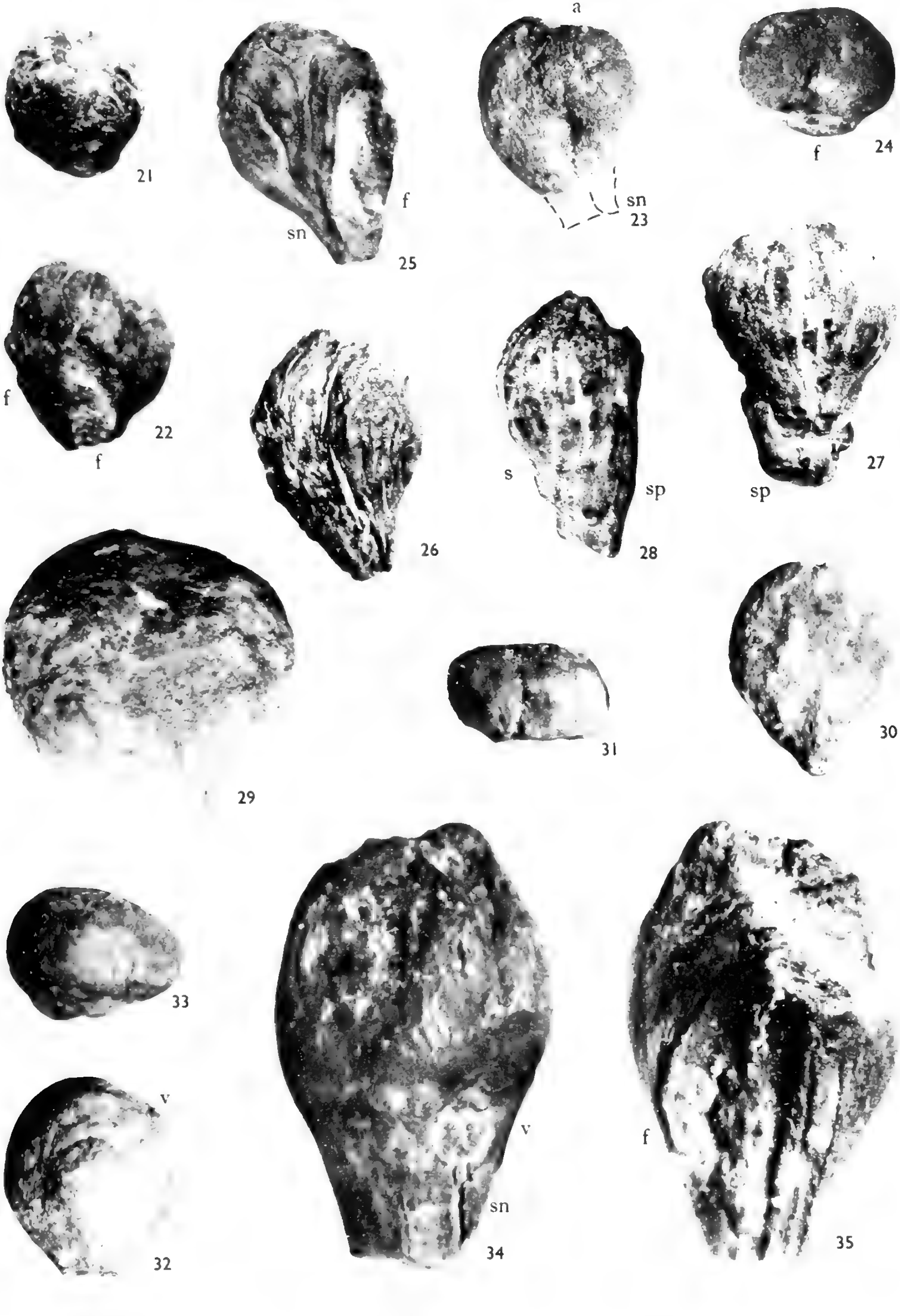
21
a
f
sn
23
24
25
22
26
s
sp
28
27
29
30
31
33
v
32
34
35

PLATE 4

Behuninia joannei gen. et sp. n.

FIG. 36. Large pair of seeds with clearly marked longitudinal fibres on right seed, upper surface. Left seed much damaged. $\times 2{\cdot}2$. (12.)

FIG. 37. Pair of seeds, *s*, attached to sporophyll, *sp*, lower surface showing rachis flanked by projecting lamina with thickened rim, *r*. $\times 3$ approx. (19.)

FIG. 38. Pair of much battered seeds, lower surface, showing subcircular areas of unknown nature but possibly due to inflation of small tracts between sunk nerves. $\times 3$ approx. (11.)

FIGS. 39, 40. Opposite sides of a pair of unequally developed seeds, *s*, Fig. 39, lower surface, showing typical fibres with anastomozing transverse branches. A bud-like structure is seen at *b*; *r*, is rachis. Fig. 40 shows the upper surface. $\times 2$ approx. (13.)

FIGS. 41, 42. Smooth obovoid detached seed with external fibres clearly displayed. Fig. 41 attachment side with facet, *f*. Fig. 42, opposite side, fibres converging to subapical micropyle. $\times 2{\cdot}5$. (6.)

FIG. 43. Another, similarly preserved. Margin of attachment facet seen at *f*. Micropyle indicated by convergence of fibres on right. $\times 3$. (15.)

? Family ***Cycadales.*** Genus ?

FIG. 44. Part of one limb of a dorsiventral scale with remains of a seed, *s*, (broken distally) embedded in a crenature of the limb with claw-like edges, *cl*. Broken end of limb at *b*. (cf. text-fig. 3). $\times 1{\cdot}5$. (21.)

FIG. 45. Opposite side of same showing marginal rim of seed. Lettering as in fig. 44. $\times 2{\cdot}2$.

FIG. 46. Same, looking onto section of fractured seed, *s*. Shallower edge of crenature which holds seed and more inflated rimmed side of seed are on the right. *cl*, claws; outer claw of crenature at base of figure, inner at top. $\times 1{\cdot}5$.

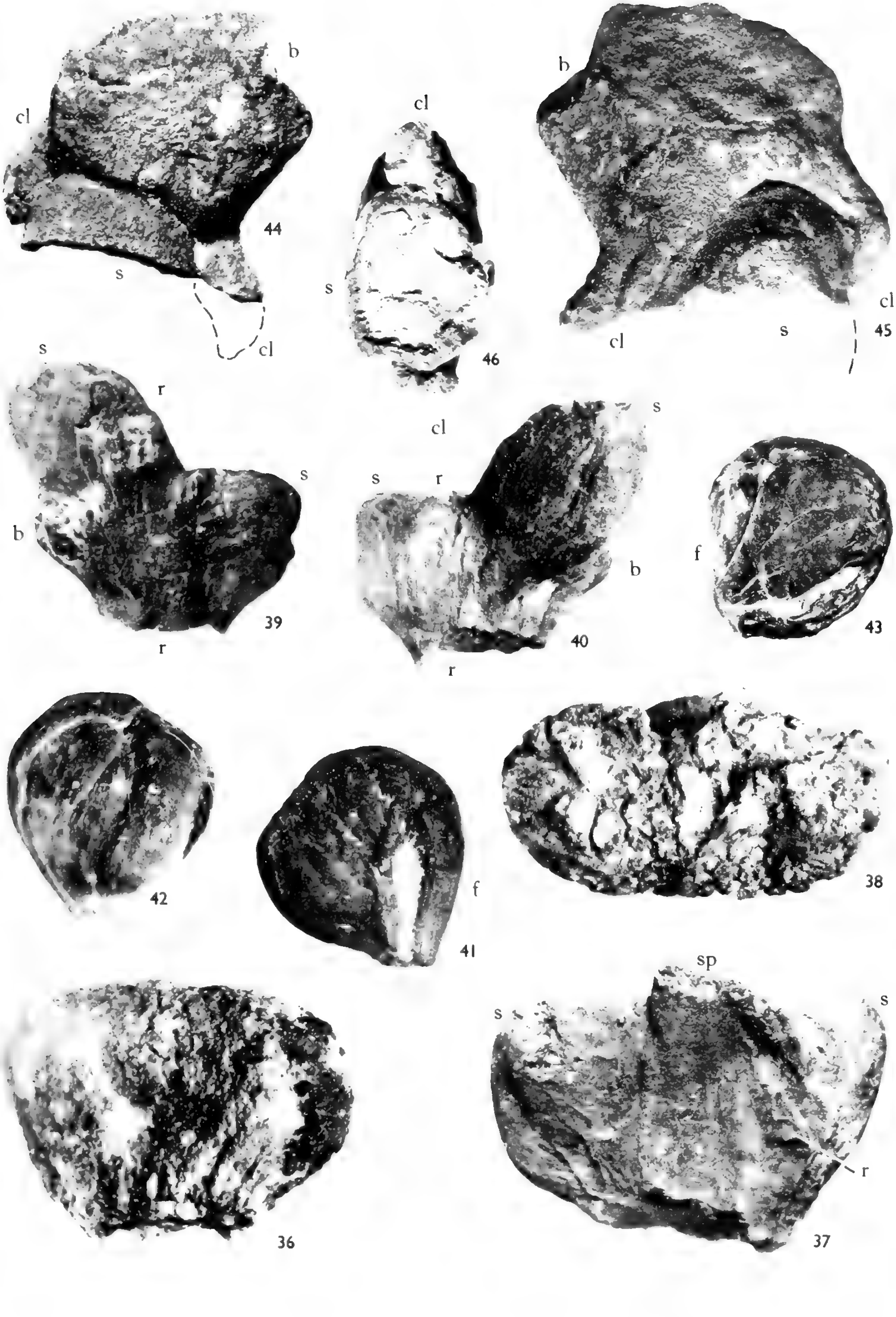
b
cl
44
s
cl
cl
s
46
b
cl
s
cl
45
s
r
s
b
39
r
cl
s
s
r
b
40
r
f
43
42
f
41
38
sp
s
s
r
36
37

PLATE 5

Jensensispermum redmondi gen. et sp. n.

FIGS. 47–49. Syntype. A seed apparently referable to this species with most of the integument so rarely preserved. Fig. 47, side view, micropylar end at *m* tending to split transversely into two jaw-like portions, *uj*, *lj*. *l* a cast of a lateral cavity. The jaw labelled *uj* is here depicted as representing the upper side of the seed but it is possible that the discovery of an infructescence may show that this position must be reversed. *a*, attachment area. Fig. 48 shows the " lower " jaw. Lettering as above. Fig. 49 shows the " upper " jaw. Some small depressions on the right are nearer to the micropylar end than in fig. 48. All the above ×6·5. (22.)

FIG. 50. Syntype. A typical abraded seed which has lost its integument showing elongate form. Looking onto " upper " (chalaza) side. Hilum to left as this seed contracts towards it. The two depressions on the left separated by a short ridge may be due to the lateral cavities. ×6·5. (24.)

FIG. 51. Syntype. Side view of an abraded seed with fibrous pulpy layers of integument exposed. *m*, micropyle, splitting into two jaws has started here. *r*, marks the limits of the hilar-chalazal region, *ch*, on the left (dark in figure), the endosperm lying to the right. *h*, approximate position of hilum. ×6·5. (23.)

FIG. 52. Seed, looking onto micropyle, abraded so that fibrous pulpy layers of the integument *f*, are exposed. Transverse split at *m* overlies the micropyle. ×6·5. (V.51599.)

FIG. 53. Syntype. Seed looking onto micropyle. Endosperm still partly covered by pulpy fibres but sufficiently abraded for embryo scar, *m*, to be exposed with fibres diverging from it. ×6·5. (30.)

FIG. 54. Another, side view, showing diagonally the junction of chalaza, *ch*, and endosperm, *a*. End of embryo vesicle seen at *e*. *h*, hilar area. Rugose surface of chalaza clearly seen. ×6·5. (V.51601.)

FIG. 55. Syntype. Seed, side, looking onto junction (vertical line) of endosperm (left) and chalazal region (right). Flattened area at top is hilar area in profile. ×6·5. (25.)

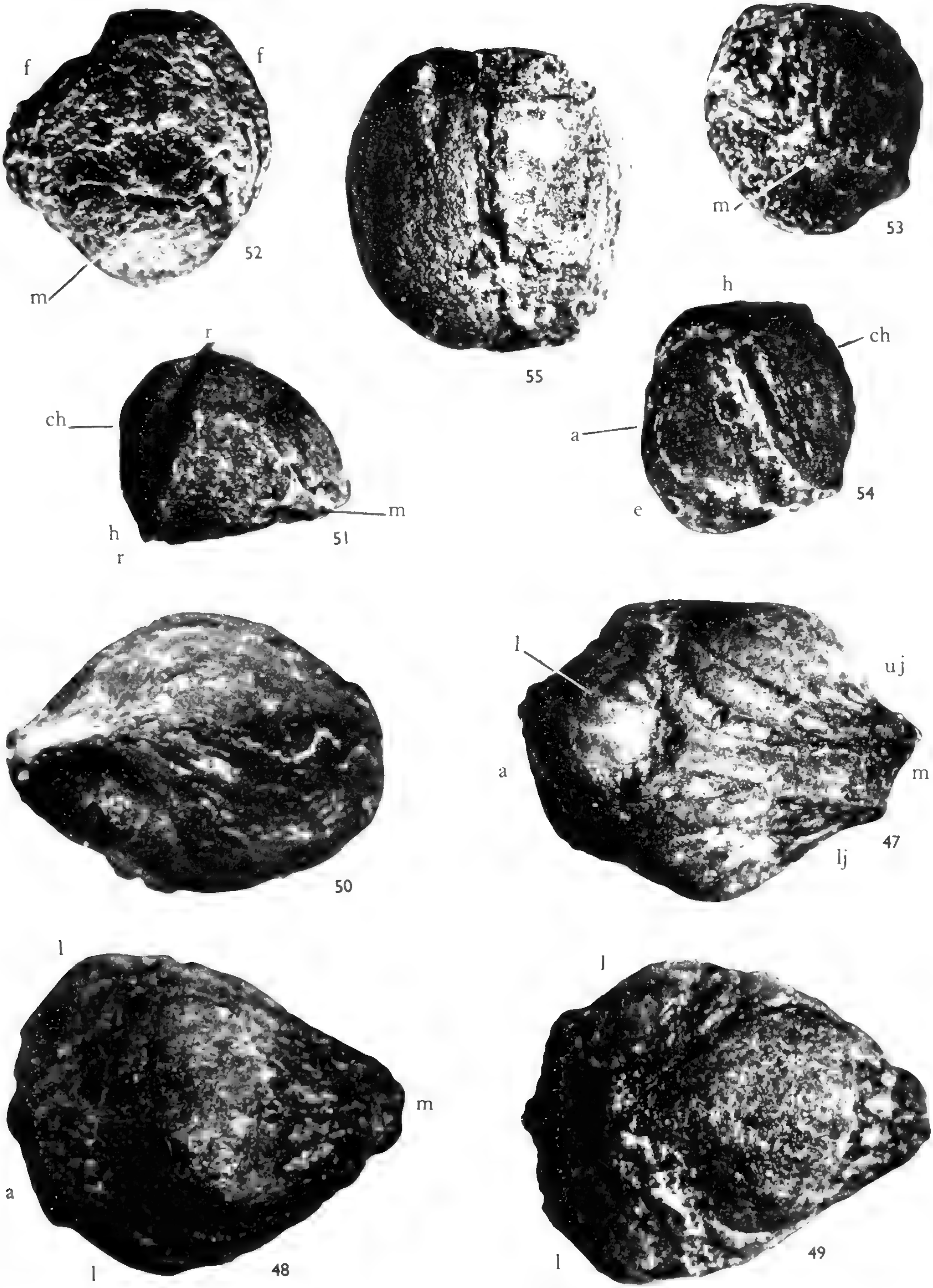
f
f
m
52
55
m
53
h
ch
r
ch
a
m
h
r
51
e
54
l
uj
a
m
lj
47
50
l
l
m
a
l
48
l
49

PLATE 6

Jensensispermum redmondi gen. et sp. n.

FIG. 56. Same seed as in Plate 5, fig. 55. Looking onto endosperm showing conspicuous navel-like embryo vesicle at centre. $\times 2{\cdot}5$. (25.)

FIG. 57. Same. $\times 6{\cdot}5$.

FIG. 58. Same, looking onto large hilar scar superficially resembling that of some Sapindaceae. Apertures for fibres to chalazal area are seen at centre of scar and at top right near junction of chalaza, *ch*, and endosperm, *a*, with the hilar scar. $\times 6{\cdot}5$.

FIG. 59. Same, opposite end to hilum. Endosperm, *a*, occupies left half of figure, chalazal region, *ch*, occupies right half. Junction, *j*, between the two lies to left of longitudinal median diameter. $\times 6{\cdot}5$.

FIG. 60. Same, looking at chalazal region (i.e. opposite side to that in figs. 56, 57). Scar near base, due to wrinkles near edge of chalaza, does not appear to represent a seed organ. Flattening at top of figure indicates hilar scar in profile. $\times 6{\cdot}5$.

FIG. 61. Another seed with typically exposed endosperm and embryo vesicle (at centre). $\times 2{\cdot}5$. (V.51603.)

FIG. 62. Seed, side, endosperm to left sharply separated by diagonal junction from chalazal region to right. Cast of hilar cavity at apex with projection, *f*, connected with funicle fibres. $\times 6{\cdot}5$. (V.51600.)

FIG. 63. Same, looking onto cast of hilar cavity which, as lighted, appears four-sided. The projection at the top of the scar is triangular in outline with two facets separated by a verticle angle. Endosperm, *a*, occupies the lower part of the figure. Junction with chalazal region above is seen at *j*. $\times 6{\cdot}5$.

FIG. 64. Syntype. Seed, side, hilar area, *h*, seen at apex is hollowed. *ch*, puckered retracted chalazal region distinctly separated by diagonal rounded margin from contracted endosperm. Embryo vesicle at point, *m* (cf. Text-fig. 17). $\times 6{\cdot}5$. (26.)

FIGS. 65, 66. Seed. Fig. 65 looking onto endosperm. Central embryo scar obscure in figure, clear in specimen. *h*, edge of hilar area; *ch*, edge of chalaza. Fig. 66 looking onto fibrous chalaza region; *h*, hilar area. $\times 6{\cdot}5$. (32.)

PLATE 6

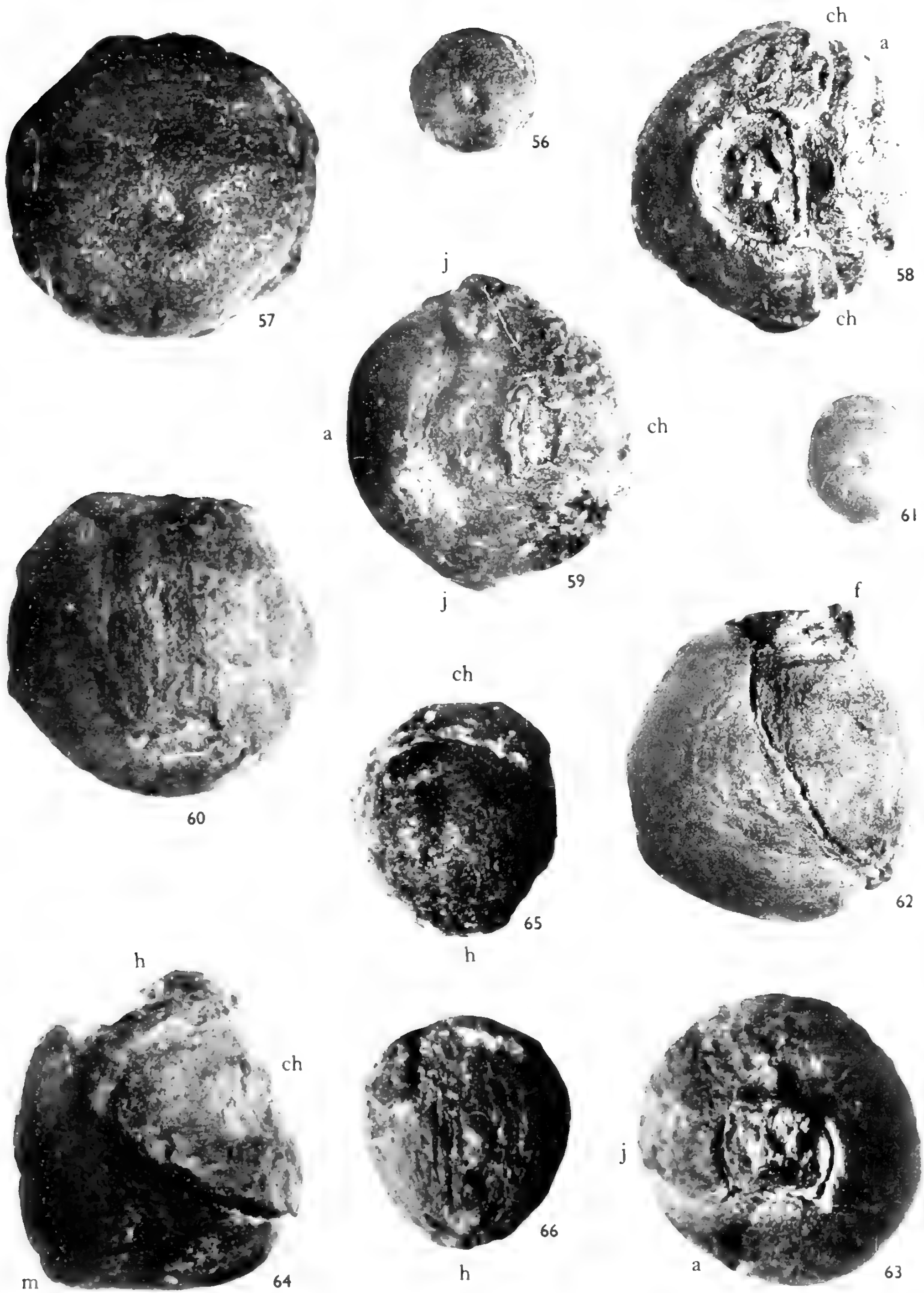

PLATE 7

Jensensispermum redmondi gen. et sp. n.

FIG. 67. Seed, Endosperm on left. Puckering of endosperm, due to contraction, is seen at junction, *j*, with chalaza. Embryo vesicle a deeply sunk pit seen obscurely on left (almost in profile). Chalazal area somewhat abraded. Remains of hilar region form a projection at top of figure. ×6·5. (V.51604.)

FIG. 68. Syntype. Seed, looking onto abraded chalazal region, the circular junction with endosperm is clearly shown as are fine (white) nerves which radiate over the endosperm from this junction. Worn hilar region lies between *h*, *h*. ×6·5. (29.)

FIG. 69. Seed with chalazal region, *ch*, largely abraded, exposing rounded extent of the endosperm (above). The specimen shows nerves diverging from chalaza over endosperm but these are obscure in the figure. *h*, position of hilum. ×6·5. (V.51602.)

FIG. 70. Syntype. Endosperm of a seed seen from much abraded chalaza side. Hollowed rim of the endosperm surrounds the small central fibrous chalazal remains. Embryo vesicle is at centre of rounded endosperm surface on which specimen lies. Hilar scar (abraded) lay towards top of figure. ×6·5. (27.)

FIG. 71. Seed looking onto endosperm with conspicuous embryo vesicle, *e*. Ridge across the endosperm below it is due to faulty preservation. ×6·5. (31.)

FIG. 72. Seed in Plate 5, fig. 54. looking onto endosperm with plug of embryo vesicle slightly extruded (centre). Hilar scar, *h*, seen in profile. Elsewhere margin of seed formed by edges of chalaza. ×6·5. (V.51601.)

FIG. 73. Seed, side. Vertical junction, *j*, of endosperm (left) with chalazal region clear. Flattened cast of hilar cavity at *h*. Slight depression, centre left, position of embryo vesicle. Longitudinally rugose surface of chalazal region due to sunk fibres clearly seen. ×6·5. (V.51605.)

FIG. 74. Syntype. Seed tilted to show surface of cast of shallow hilar cavity. Chalazal region below with well preserved surface showing longitudinal fibres diverging from hilar area and arising beneath cast of hilar cavity. Limits of endosperm at *a*, *a*. ×6·5. (28.)


J
67
e
71
h
72
h
73
69
ch
a
a
74
h
68
h
70

PLATE 8

Sequoia sp.

FIG. 75. Cone cast looking onto narrower diameter. Shows spirally arranged lozenge-shaped scales broader than high with transverse ridge or furrow. Scales outlined by darker calcite ridges. Short stalk seen at base. ×3 approx. (38.)

FIG. 76. Same, turned to left through 90°, looking onto broader diameter. ×2·6.

FIG. 77. Larger cone, scales represented by featureless light grey calcite outlined by darker ridges between them. Tilted slightly so that part of apex is visible in shadow. A line of fracture runs transversely from *c* to *c*. ×2. (39.)

FIG. 78. Same, looking onto transversely fractured surface (lower portion) showing obscure outlines of the flat seeds in dark calcite contrasting with lighter calcite beyond and between them. Surface of cone seen in fig. 77 is towards base of figure. ×2·6.

FIG. 79. Less well preserved cone, side. ×2·6. (V.51617.)

Hillistrobus axelrodi gen. et sp. n.

FIG. 80. Syntype. Small almost perfect cone, extreme tips of most scales slightly imperfect. ×2·5. (40.)

FIG. 81. Syntype. Larger crushed cone. ×3 approx. (41.)

FIGS. 82, 83. Opposite sides of an imperfect cone, lower half missing. Fig. 82 shows elongate scale tips. Fig. 83 shows the opposite side of the cone with scales abraded so that the attenuated tips are worn away. ×2·6. (V.51618.)

FIG. 84. Cone fragment, near base. ×2·5. (45.)

FIG. 85. Syntype. Lower part of more elongate cone showing attenuated scale tips merging below into foliage-like scales. ×2·6. (42.)

FIG. 86. Twig which may have borne a cone at the tip. Leaves may be compared with basal scales in fig. 85. ×2·6. (43.)

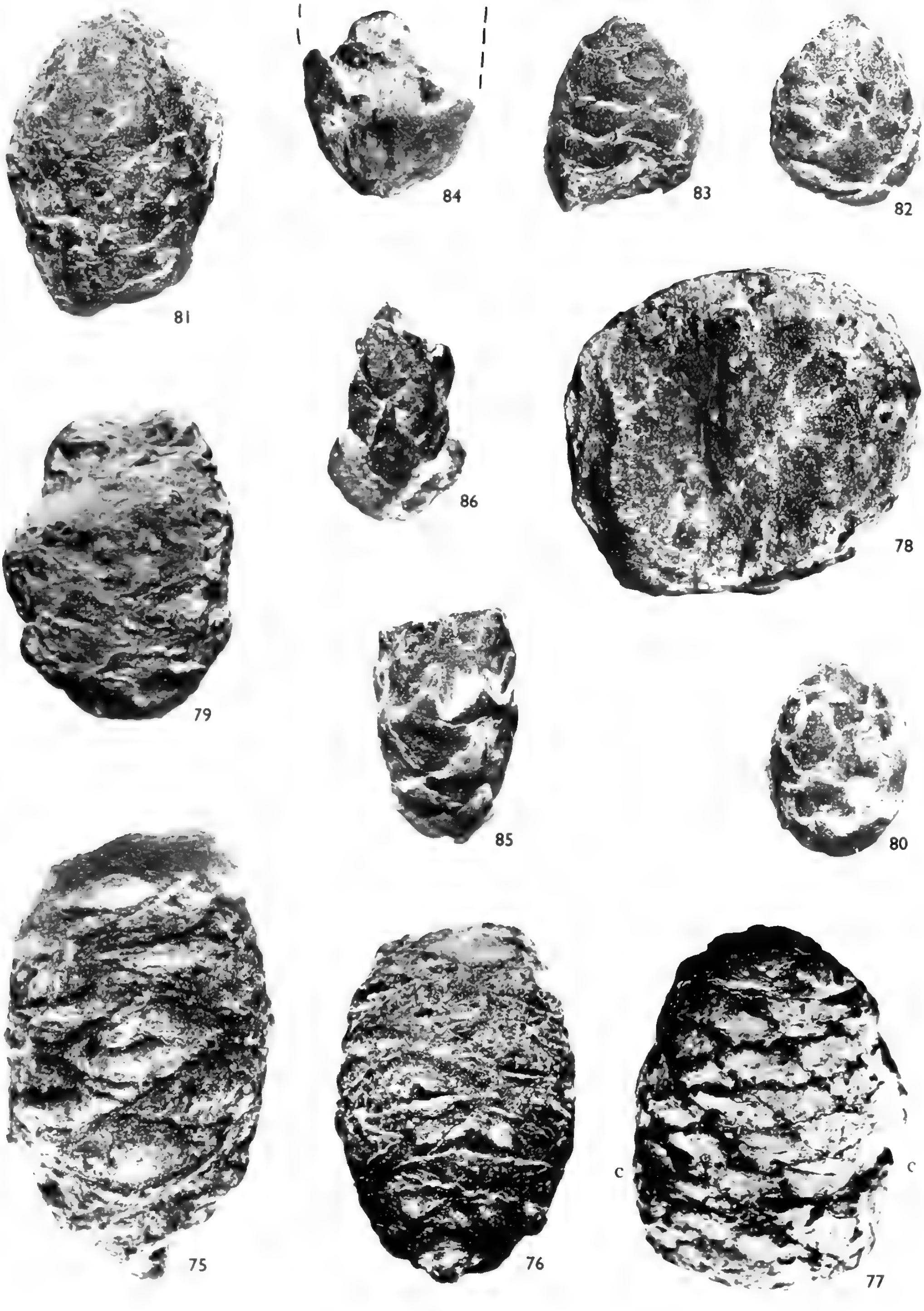
84
83
82
81
86
78
79
85
80
75
76
c
c
77

PLATE 9

Hillistrobus axelrodi gen. et sp. n.

FIG. 87. Lower part of larger cone transversely fractured showing the thin overlapping scales with concave upper and angled lower surface and attenuated margins. ×3. (44.)

Genus ?

FIG. 88. Much abraded cone with scales worn so that apices are gone exposing thickened central part. Possibly this species. ×2·6. (48.)

Genus ?

FIG. 89. Battered cone with small spirally arranged scales. ×2·6. (49.)

Carpolithus provoensis sp. n.

FIG. 90. Holotype. Integument or cupule, side view showing two basal facets near *f*, and truncated apex. ×1·9. (50.)

FIG. 91. Same, opposite side, with furrow at base. ×1·5.

FIG. 92. Same, apex, showing pointed segments, 1 to 5 partially obscured by matrix. ×1·6.

Carpolithus radiatus sp. n.

FIGS. 93–95. Syntype. Seed. Fig. 93, concave apex of peltate radially furrowed integument. Fig. 94, side showing contraction into stalk. Fig. 95, base looking onto broken stalk. ×2·2. (51.)

FIGS. 96–98. Another specimen with sharply angled circumference (abraded). Fig. 96, apex; fig. 97, side; fig. 98, base showing very slender stalk and radial furrows. ×2 approx. (52.)

FIGS. 99–101. Another. Fig. 99, apex; fig. 100, side; fig. 101, base. ×2 approx. (V.51619.)

FIGS. 102–104. Abraded poorly preserved specimen. Fig. 102, apex with outline of horizontal albuminous seed cast. It shows central depression connected by channel with margin. Fig. 103, base, fig. 104, side (stalk broken off short). ×2 approx. (V.51620.)

PLATE 9

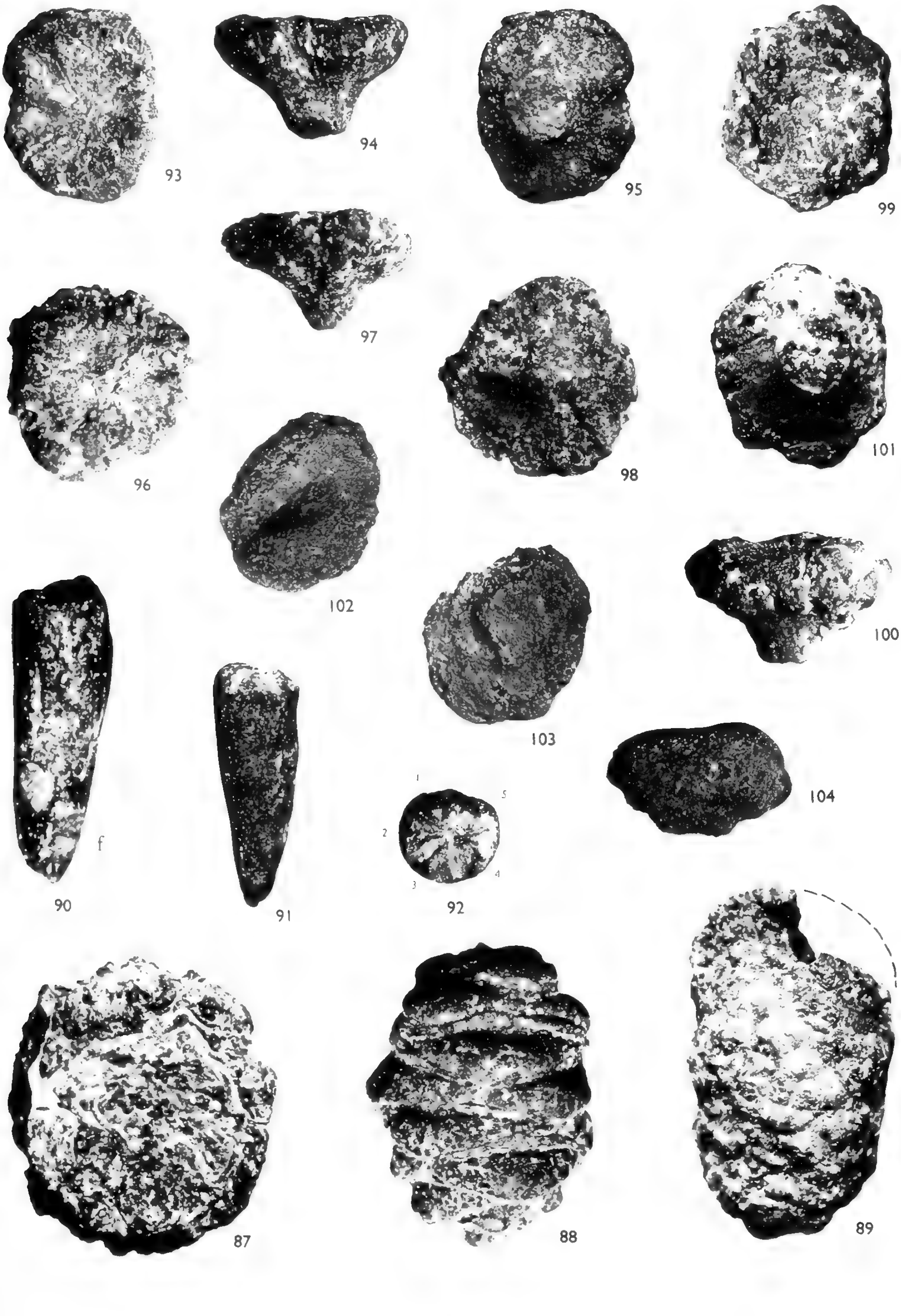

PLATE 10

Carpolithus radiatus sp. n.

FIGS. 105–107. Syntype. Peltate seed with lateral bud arising from stalk and albuminous seed cast exposed at apex. Fig. 105, apex, showing tip of bud, *b*, and seed cast with central depression connected by a canal with margin of integument. Fig. 106, side view, bud arising on left. Fig. 107, base with thick broken stalk, bud on left. ×2 approx. (53.)

FIGS. 108–110. Seed with much thickened disc-like form. Fig. 108, apex, with indication of central micropyle. Fig. 109, side, showing thickness of disc. Fig. 110, base. ×2 approx. (V.51621.)

FIGS. 111–113. Seed with stalk and part of integument broken away. Fig. 111, apex; seed cast (= endosperm) exposed at *s*. White spot at centre indicates micropyle. Fig. 112, side, seed cast exposed below equator. Fig. 113, opposite side, tilted to bring concave apex with micropyle (white) into view. Seed cast exposed in shadow below *s*, *s*. ×2 approx. (V.51622.)

FIGS. 114–116. A dorsiventrally thick specimen. Fig. 114, apex. The tangential cut due to embedded stick suggests fleshy texture of endosperm. Fig. 115, side. Fig. 116, base. ×2 approx. (54.)

FIG. 117. Seed, apex, possibly with embryo scar (central white spot). ×2 approx. (55.)

FIG. 118. Base of a seed showing stalk with radial structure. ×2 approx. (56.)

FIGS. 119, 120. Syntype. Fig. 119, apex of seed with small central scar indicating micropyle (embryo vesicle ?). Fig. 120, base from which stalk and integument have been abraded showing rugose surface of chalazal region (cf. *Jensensispermum*). *h*, position of hilum. ×2 approx. (58.)

FIGS. 121, 122. Syntype. Twinned seeds. Fig. 121, apex; *s*, *s*, line of separation between two closely adpressed seeds. Fig. 122, base, lettering as above. ×2 approx. (59.)

FIGS. 123, 124. A peltate disc which has been fractured longitudinally before fossilization. Fig. 123, side, exterior. Fig. 124, fractured surface showing fibrous axis with pair of fibre strands. ×2 approx. (57.)

FIGS. 125, 126. Another longitudinally fractured disc with median fibres. Fig. 125, exterior; fig. 126, fractured surface on which a median canal is seen. ×2 approx. (V.51623.)

FIGS. 127, 128. Syntype. Peltate disc with marked apical mucro fractured as in preceding. Fig. 127, exterior; fig. 128, fractured surface with axis terminating in mucro flanked by shallow radial cavities. ×3 approx. (60.)

FIGS. 129, 130. Club-shaped head (immature seed or barren shoot tip). Fig. 129, apex with diverging fibres. Fig. 130, side. ×3 approx. (61.)

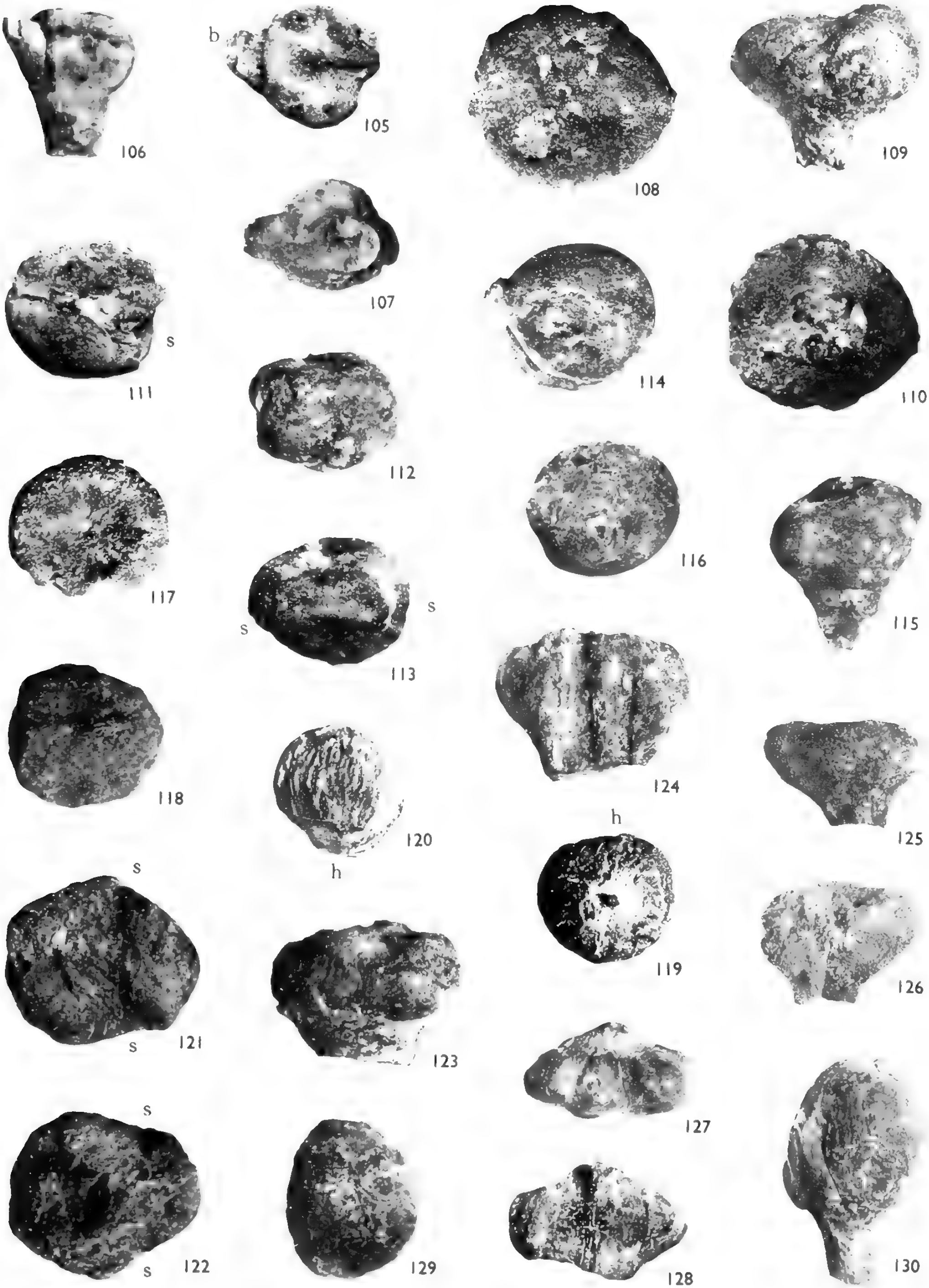
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PLATE 11

Carpolithus spp.

FIG. 131. Seed enclosed in a cupule which bears four unequal rounded segments above, of which two adjacent ones are small. Apical view. ×1 approx. (66.)

FIG. 132. Same, base abraded so that the seed is exposed through a gap in cupule. ×1 approx.

FIG. 133. Another, apex much flattened, three segments above. Junction of lobes, *j*, obscure in figure clearer in specimen. ×1 approx. (67.)

FIG. 134. Same, base, more or less uncrushed with projecting central attachment. ×1 approx.

FIGS. 135, 136. Opposite sides of a fibrous striate "fruit", broken at one end. ×1·5. (68.)

FIGS. 137, 138. Another, opposite sides, pointed at both ends (both slightly imperfect). ×1·5. (V.51628.)

FIGS. 139, 140. Another with expanded base (crushed cupule or sucker-like attachment), opposite sides. ×1·6. (69.)

FIGS. 141, 142. Similar but larger specimen broken at tip; opposite sides. ×1·6. (70.)

FIGS. 143, 144. Another broken at one end, opposite sides. ×1·6. (71.)

FIG. 145. Specimen pointed at both ends. ×1·5. (72.)

FIG. 146. Specimen, nature unknown, presenting a false appearance of a rimmed pod. ×1·6. (75.)

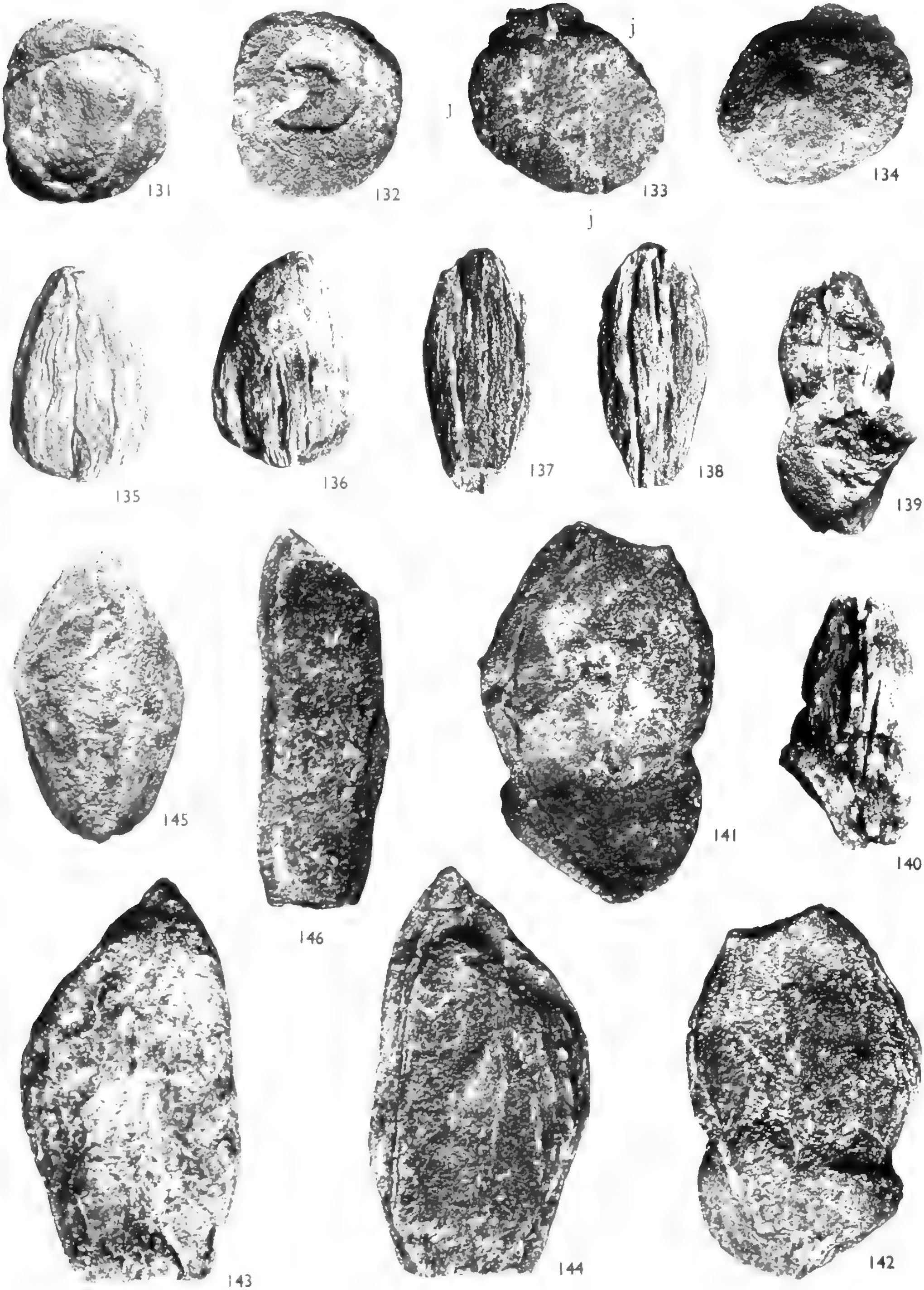
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PLATE 12

FIG. 147. Twinned algal or fungal body showing superficial concentric striae. $\times 1 \cdot 6$. (76.)

FIGS. 148, 149. Opposite sides of another alga, fungus or tuber. Fig. 149 cut off on right by edge of plate. $\times 1 \cdot 6$. (77.)

FIGS. 150, 151. Large flattened algal-like object with clearly marked concentric structure and irregular pitting at centre of both surfaces. Opposite sides. $\times 1 \cdot 6$. (78.)

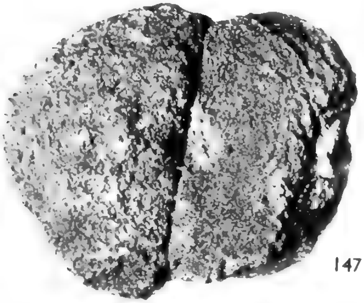
FIG. 152. Similar body which had been fractured showing crystal-filled cavity without internal structure. Part of specimen cut off by edge of plate on left. $\times 1 \cdot 6$. (79.)

FIGS. 153, 154. A curved obconical fragment of unknown affinity which appears to have been split longitudinally, the other half being missing. Fibrous radial structure is seen on the exterior (fig. 153). Tendency to shred and weather along the fibrous lines may be seen. Fig. 154 shows the plane of fracture. In both figures the curved convex surface is seen at the apex. $\times 1 \cdot 6$. (80.)

FIG. 155. A detached thorn (unknown affinity). The point, *p*, is down curved. The broad elliptical base with slightly convex surface is seen on left. Its limits at the top of the figure are indicated by *b*, and at the base of the figure are clearly outlined against the shadow. $\times 1 \cdot 6$. (81.)

FIG. 156. Subglobular body with the exterior splitting into petal-like segments. Possibly fungoid. $\times 1 \cdot 6$. (82.)

FIG. 157. Object bearing misleading resemblance to a flattened subcircular pod. $\times 1 \cdot 6$. (83.)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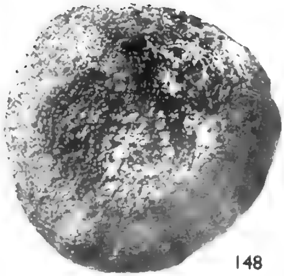
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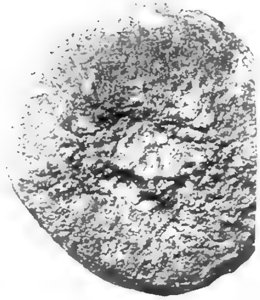
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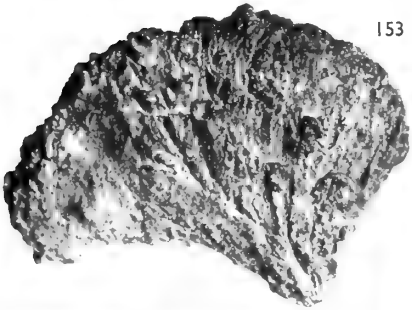
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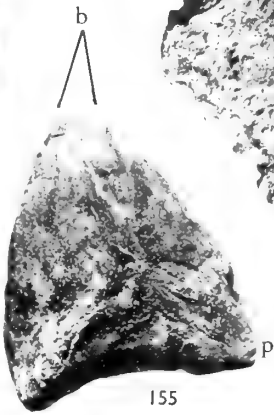

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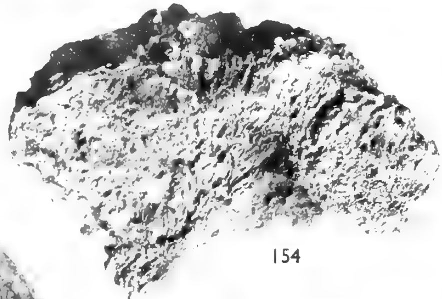
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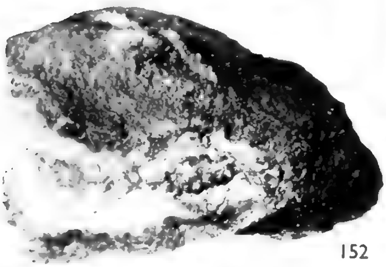
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NATURAL HISTORY

SILICIFIED PRODUCTOIDS FROM THE VISEAN OF COUNTY FERMANAGH

C. H. C. BRUNTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 12 No. 5
LONDON: 1966

SILICIFIED PRODUCTOIDS FROM THE VISEAN OF COUNTY FERMANAGH

BY

CHARLES HOWARD CAMPBELL BRUNTON, Ph.D.

Pp. 173–243 ; 19 *Plates* ; 11 *Text-figures*

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SILICIFIED PRODUCTOIDS FROM THE VISEAN OF COUNTY FERMANAGH

By C. H. C. BRUNTON

CONTENTS

I. SYNOPSIS

Visean limestones exposed to the south-west of Lower Lough Erne in county Fermanagh, Northern Ireland, have yielded a silicified fauna rich in brachiopods and bryozoans. The brachiopods will be described in a series of papers of which this is the first and deals with the productoids. Fourteen genera are represented including 4 new species. The Strophalosiidae are believed to be the first recorded from the Lower Carboniferous rocks of the British Isles. Heteralosiinae is placed into junior synonymy with Strophalosiinae and a new subfamily,

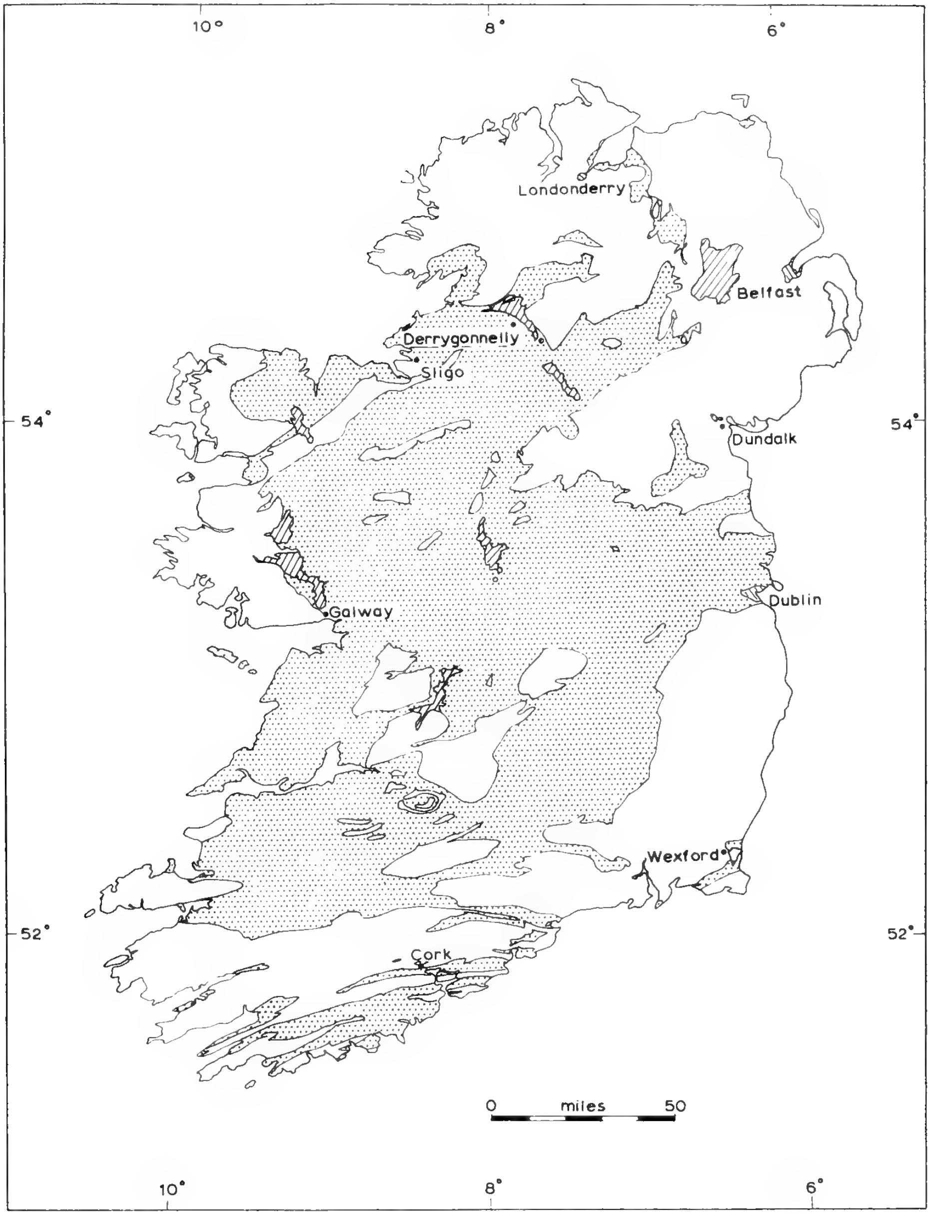

FIG. 1. Map of Ireland showing the position of Derrygonelly, from near which the faunas were collected, in relation to the Carboniferous rocks (dotted).

Dasyalosiinae, is erected for completely spinose strophalosiids. Juvenile shells have revealed structures indicating a closer relationship between the productoids and chonetoids than is commonly accepted.

II. INTRODUCTION AND ACKNOWLEDGMENTS

DESPITE being the area from which Phillips collected several of the type specimens described in his work of 1836, county Fermanagh has received little geological attention until recent years. The area from which the author has made faunal collections lies to the south of Lower Lough Erne, about 12 miles west-north-west of Enniskillen and close to Bunnahone and Carrick Loughs. A prominent crescent of hills composed of chert bearing or reefal limestone, generally identified as the Dartry Limestone group, forms a topographic feature throughout the counties of Sligo, Leitrim and Fermanagh.

Geologically this area of county Fermanagh falls between the Sligo syncline to the south-west (Oswald 1955), and the Omagh syncline to the north-east (Simpson 1955). While being closely comparable to the Sligo syncline stratigraphically, the area also shows transitional features between these two adjoining regions. In recent years Turner (1951), Padget (1952, 1953), George (1953), Oswald (1955), Simpson (1955), George & Oswald (1957) and Schwarzacher (1961) have described areas surrounding mid-Fermanagh or touched upon its geology in general terms. However, the area has not been described since the mapping of the Geological Survey of Ireland (Symes & Wilkinson 1886). These authors recognized the main elements of the stratigraphy and assigned them to Lower, Middle and Upper groups of the Carboniferous. The argillaceous limestones and shales were termed " calp ", and this name lingers on to the present. The reefal limestones were not differentiated, although it was recognized that the cliffs of Knochmore are " so massive that it is hard to detect bedding ". Within the studied area only one fossiliferous locality (Symes & Wilkinson 1886 : 18, locality 7) was mentioned, and from it only crinoids and *Pentremites* were listed. The following 15 species of brachiopods were recorded of which only 4* came from localities close to the present area :

**Athyris ambigua*	*Rhynchonella pleurodon*
Athyris planosulcata	**Spirifera bisulcata*
Chonetes hardrensis	**Spirifera glabra*
Orthis resupinata	*Spirifera striata*
Productus giganteus	*Spiriferina cristata*
Productus punctatus	*Streptorhynchus crenistria*
Productus scabriculus	**Terebratula hastata*
Productus semireticulatus	

A further 7 species from the Carboniferous rocks of Sligo and Leitrim were reported by Symes & Wilkinson (1885 : 33):

Chonetes papilionacea	*Productus margaritacea*
Orthis michelini	*Spirifera laminosa*
Productus aculeatus	*Spirifera pinguis*
Productus fimbriatus	

The 7 productoid species listed above, and collected from a wide area, compare with the 16 species of this group recovered from beds at about the same stratigraphic level at Bunnahone and Carrick Loughs.

The local stratigraphy consists of a predominantly argillaceous and calcareous series, referable to the uppermost Benbulben Shale and the Glencar Limestone of Oswald (1955), which occurs below the Dartry group. These boundaries are gradational and poorly fixed, as is that between the Glencar Limestone and the non-reefal Dartry Limestone. The reef limestones are based upon the Glencar rocks but are developed principally within the overlying Dartry group. It is from a single limestone bed towards the top of the Glencar series that the bulk of the silicified faunas has been collected. The limestone bed, between 21 and 23 cm. thick, crops out on the south side and across the bed of the Sillees river, about 250 yards downstream from the old exit of Bunnahone Lough (Text-fig. 2). During the winter of 1962–63

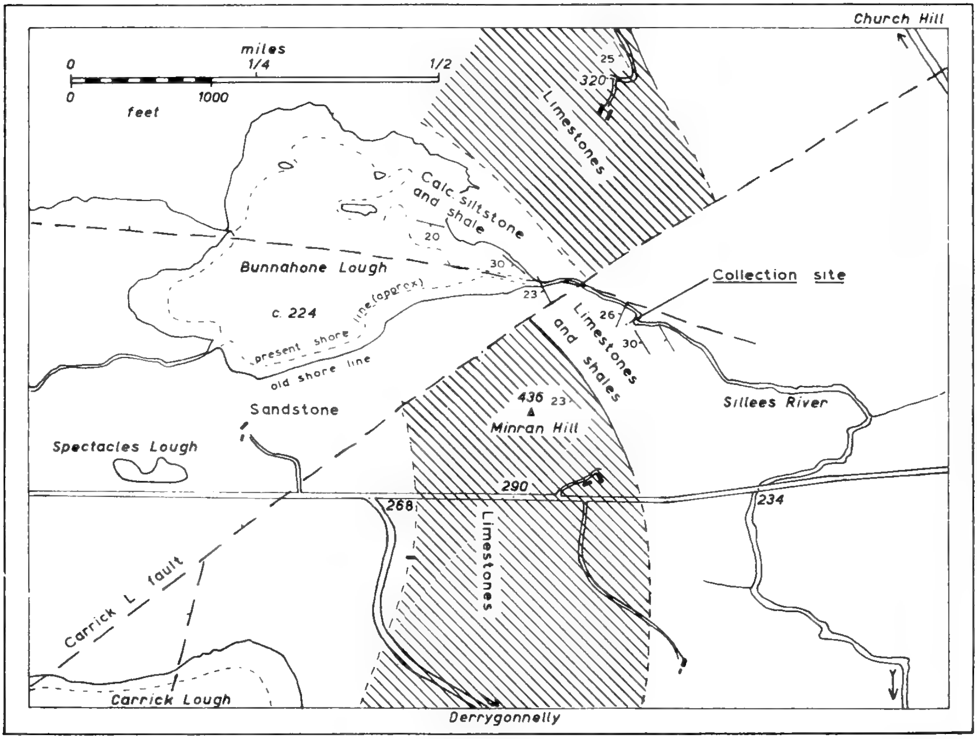

FIG. 2. Map of the Bunnahone region showing the site by the Sillees river from which the silicified faunas were collected. Minran hill is the most northerly of the exposed reef-knolls in the Dartry Limestone (shaded) of this region in Co. Fermanagh. Reefal limestones are again exposed on the south shore of Carrick Lough and subsidiary collections were made there. The shore-lines of both loughs are as on the 6-inch Ordnance Survey maps, but dredging has lowered the water levels so that their shores have receded to approximately that shown by the dashed lines.

Faults in bold dashed lines; heights in feet.

the level of the Lough water was lowered by about 3 feet so that in normal climatic conditions the length of the river is now extended, for approximately 75 yards westwards over the old Lough floor. The lower one-third of the limestone bed is muddy, containing " pebbles " comparable to the " limestone conglomerate " of Schwarzacher (1961 : 1495). Above this the bed becomes a clean biomicrite and yields a rich fauna. The top few cm. are again muddy and sparsely fossiliferous.

The reefal and non-reefal facies of the Dartry group are strongly contrasting. The reefal areas of Carrick, Knockmore and Killydrum are similar to those of north-east England described by several authors, including Bond (1949, 1950) and Black (1950, 1953, 1954). These rocks contain a brachiopod fauna that differs from those collected from the underlying limestones. The whole of the Dartry exposure, in this region of Fermanagh, becomes regularly bedded and commonly slightly chert-bearing before the deposition of the shales and sandstones at the top of the local succession.

Limestone blocks with a volume of up to 15,000 cubic cm., collected from the Bunnahone area, were etched in dilute hydrochloric acid. Acetic acid was found to be much slower in action and failed to yield additional material. All the etch residues were scrutinized, in water, under a binocular microscope to avoid the loss of minute specimens. The labour of this has been rewarded by the collection of juvenile valves of several species which show structures hitherto unrecorded.

Statistical methods have been applied whenever the size of the sample was sufficiently large and well preserved to allow for quantitative studies in variation. Williams (1962) has discussed the use of statistics as a tool in the taxonomic study of brachiopods and some of the procedures advocated by him have been followed. Paired measurements of skeletal attributes have been converted into estimates of growth and variability by the use of bivariate analysis techniques of Kermack & Haldane (1950). The statistical tables presented here give the mean of each attribute and its variance; "r", the coefficient of correlation between the attributes, and "a", the growth ratio between the variable attributes, together with its variance. Where allometry affected the sample the data is presented in the form Log_e. In comparisons of external ribbing Williams (1962) use of the nouns costae and costellae have been used, viz. costa = a primary rib, "originating at the protegulal node ; and costella = a secondary rib, one which arises by branching or intercalation anterior to the umbonal zone".

I wish to thank Professor A. Williams for all his assistance during my study of the Fermanagh brachiopods while working in his department at Queen's University, Belfast, and for reading the manuscript. I am grateful to Dr. H. M. Muir-Wood of the British Museum (Natural History), Professor J. Mitchell of Galway University College, and Dr. G. A. Cooper of the United States National Museum for their co-operation in lending specimens in their care ; to them, and to all those who have assisted in numerous ways I extend my thanks.

III. PRODUCTOID MORPHOLOGY

The Strophalosiacea and Productacea here described form part of a rich and well preserved brachiopod fauna. The fine silicification of these shells has enabled the

study of interiors that were previously poorly known and of juvenile structures hitherto unrecorded. The faunas comprise shells and valves of a wide size range so that ontogenetic variation in features, such as the cardinal process, has been possible.

While it is hoped to deal at greater length elsewhere with these features, a few brief remarks regarding the more important points that have emerged from this study should be mentioned. Perhaps the most important contribution to our knowledge of brachiopod faunas is that gained from the well preserved juvenile valves. Small spines that curl in a clasping fashion around the ventral umbo of productaceans have been recognized for a long time, but it now seems clear that all the genera here described were furnished with such spines. Their development was most probably genetically controlled, but their growth was capable of alteration in response to foreign objects. Moreover, it has now been demonstrated that at least some juvenile species of *Productina*, *Krotovia*, *Plicatifera*, *Eomarginifera* and *Avonia* possessed a pedicle sheath (Brunton 1965) and this is mentioned under the species concerned and figured in the present work (Pl. 7, figs. 1, 4, 5). Until now the supposed absence of a

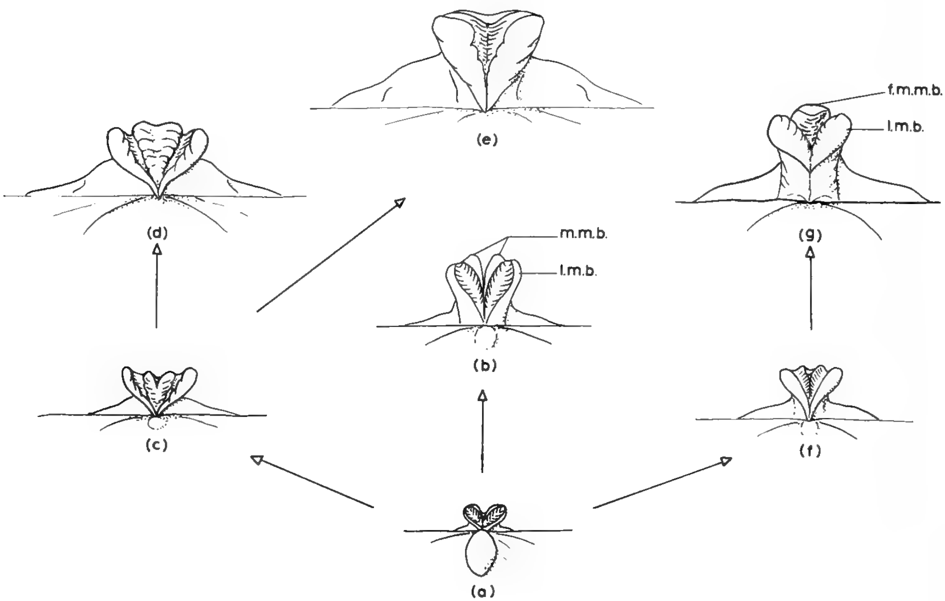

FIG. 3. Stylized illustrations of four principal ontogenetic trends in the development of the productoid cardinal process. (a) : generalized juvenile stage with the two myophore lobes well separated. The diductor muscle bases, accommodated on each lobe, are enclosed by shelly muscle boundaries ; *l.m.b* : lateral muscle boundary ; *m.m.b.* : median muscle boundary. (b) : adult quadrifid cardinal process ; (c) and (d) : the development of the trifid cardinal process by the fusion of the median muscle boundaries over which the diductor muscle bases spread ; (e) : excessive growth of the lateral muscle boundaries which surround the diductor muscle bases ; (f) and (g) : the development of the trifid cardinal process with a shaft by the antero-median fusion of the lateral muscle boundaries. *f.m.m.b* : fused median muscle boundaries.

pedicle sheath was taken as strong evidence for the separation of the productoids from the chonetoids and other strophomenoid stocks known to possess such a structure. It would now seem more natural to reunite these two spinose groups of the strophomenoids at subordinal level.

The presence of a pedicle sheath and juvenile clasping spines indicate that after the free larval stage, these animals were fixed in their earliest stages of development. However, many genera became more or less free-living later in life.

Ontogenetic changes to the cardinal process of most species follow distinctive patterns, but are such as to have altered its appearance considerably at different developmental stages (Text-fig. 3). Fagerstrom & Boellstorff (1964) have illustrated the changes that occurred during the ontogeny of the cardinal process of *Juresania nebrascensis* and pointed out the need for care in its use taxonomically. In the past inordinate emphasis has been placed on the cardinal process as a taxonomic criterion as a result of which inflexible nomenclature has arisen describing its various forms. A study of the cardinal process in a wide range of productoids in all growth stages shows that they are all based upon a bilobed form. The paired diductor muscle bases were attached to these two myophore lobes. The various so-called " trilobed " and " quadrilobed " processes developed as a result of a varying degree of median fusion of the basic two lobes. It is suggested, therefore, that " lobe " should be restricted to the basic structure to which muscles were attached and that the appropriate prefix with the root " fid " be employed for later developmental stages of the cardinal process. In this way the cardinal process in which the two myophore lobes had completely fused medianly should be called trifid (Text-fig. 3, d); that in which the lobes were deeply incised, but not medianly fused, should be quadrifid (Text-fig. 3, b).

Brachial impressions and the possible traces of a mantle canal system are described under the genera in which they have been observed most clearly, e.g. *Overtonia* and *Eomarginifera*.

A stylized productacean ontogeny

All extinct brachiopods probably spent a time as free planktonic larvae during which their numbers were vastly reduced by predation and other factors of a competitive environment. Some environmental or physiological stimuli induced settlement of the surviving spat on to the sea-floor, during which many more individuals were lost. It is possible, however, that the larvae had a small degree of selective power enabling them to better their chances of survival at this stage. It is believed, that in common with most strophomenoids, the productacean spat were provided with a posteriorly developed thread-like pedicle, surrounded by a short skeletal sheath, which was used to make the primary attachment to some solid object, such as skeletal debris, living material, or even large sand grains. The larval form is represented by the protegulal nodes of each valve, commonly 0·2 to 0·3 mm. long, and in some genera distinctly bipartite on the pedicle valve. The rudimentary brephic valves soon developed and the ventral one commonly had a distinct groove along its length which was about 0·2 mm. wide (Text-fig. 4, a, d). This may have been an impression left by the primary anchoring object, but it is not always so,

and it seems more likely that it resulted from a differential growth rate within the ventral valve, which perhaps reflects a juvenile development of the muscles. The first pair of spines encircled this groove, at about one-half the brephic valve length, viz. about 0·5 mm. from the beak, and were sometimes so placed as to have grown around some slender object, like a bryozoan stalk. The regularity of spine development indicates that it was genetically rather than phenotypically controlled. Two or three additional pairs of clasping spines developed close to the hinge-line, up to a distance of about 2·0 mm. apart, on the young neanic pedicle valves about 1·5 to 2 mm. long. These spines grew postero-ventrally and arched the pedicle umbo so that they occasionally encircled a piece of shelly debris (Pl. 7, figs. 1–3), commonly that to which the spat first attached itself. By this stage, 1·5 to 2 mm. long, the adult ornament of the valve was beginning to develop. As well as growth-lines, rugae and/or costae were distinguishable. Grant (1963 : 134) reports the occurrence in *Linoproductus* of clasping hinge spines having continued to form along the full width of the hinge-line throughout life, but this appears to be unusual amongst Productaceae as a whole. Up to a length of a few mm. the young shell was probably firmly anchored ; during the brephic stage by the pedicle, and later by the small spines clustered around the umbo. Later it is probable that most shells lost their

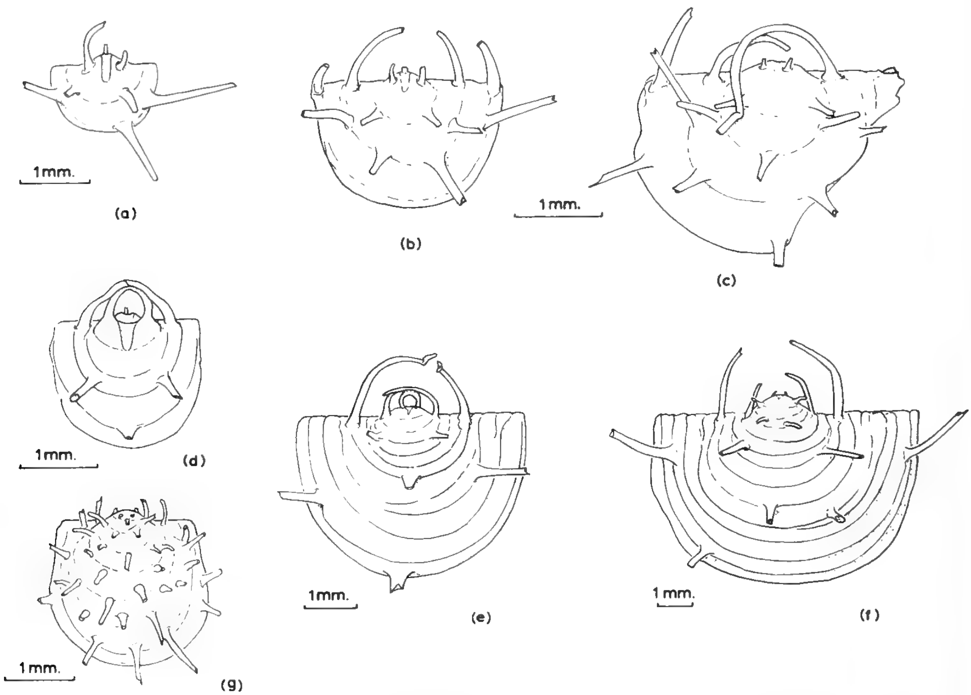

FIG. 4. Illustrations of juvenile pedicle valves : (a–c) *E.* (*Eomarginiferina*) *trispina* subgen. et sp. n. ; (d–f) *Plicatifera plicatilis* (J. de C. Sowerby) and (g) *Krotovia spinulosa* (J. Sowerby), showing patterns of spine arrangements, the posterior clasping spines, and the postero-median pedicle sheath.

firm attachment and became more or less free-living on the sea floor. There are, however, many exceptions to this, such as the scachinellids and richthofenids and those abundantly spinose genera like *Spinulicosta*, which must have grown together in crowded colonies with their spines entangling with one another ; moreover, many strophalosids remained cemented to some solid object by their pedicle valves.

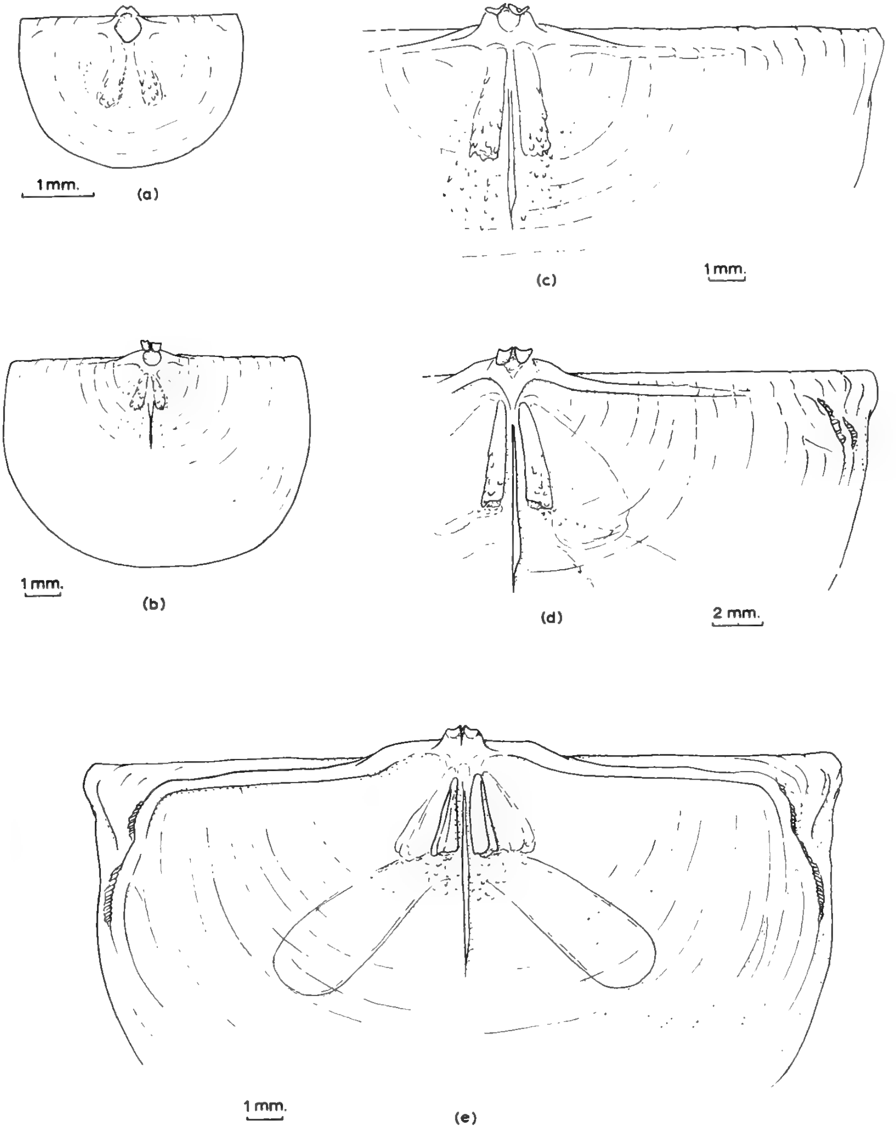

FIG. 5. Stylized illustrations, based upon *Plicatifera plicatilis* (J. de C. Sowerby), of the ontogenetic development of the productacean brachial valve interior.

Within the Fermanagh shells the cardinal process is distinguishable in the smallest available valves, 1·2 mm. long, and by about 2 mm. long the rudiments of the lateral ridges had developed (Text-fig. 5, a). The adductor scars formed next and in valves 5 mm. long the median septum was commonly distinguishable between and anterior to the adductor scars (Text-fig. 5, b). In the pedicle valve the adductor scars were commonly differentiated before the diductor scars. The small umbonal spines were sealed by secondary shell at various stages of development, leaving only the marginal spines in a living condition. The growth of the brachial valve kept pace with that of the pedicle valve and anteriorly the two curved together, but a trail was not formed until after the development of the visceral disc. Thus the onset of the trail occurred at very varied shell lengths in different genera.

Most of the Productacea have strongly curved pedicle valves and less curved brachial valves. This was achieved by the slower growth-rate of the brachial valves, which in consequence usually have a more crowded concentric ornament, e.g. rugae, lamellae or spines (Text-fig. 6). This curvature also meant that up to maturity, when the visceral disc was fully developed, the brachial valve rotated about an axis at the hinge-line. This would have led to the formation of a continued gap, or a poor fit of the posterior margin had it not been for the development of the posteriorly placed lateral ridges which extended laterally throughout growth (Text-fig. 5, c–e). Towards adulthood lateral growth close to the hinge-line accelerated in some groups and led to the formation of ears. After maturity, while a slow dorso-anterior growth continued, lateral growth commonly ceased, so that the shell gradually became more curved in profile.

If rugae had developed across the visceral region, they stopped at this stage although radial ribbing continued to the anterior margin. The brachial valve

(a) Overtonia fimbriata						
rugae	1–4	5	6	7	8	9
brachial valve	2·7	3·6	4·5	5·3	6·3	7·5
pedicle valve	3·3	4·8	6·6	8·8	11·6	12·6

(b) Avonia (Quasiavonia) aculeata			
brachial valve	4·5	6·0	7·0
pedicle valve	6·0	8·0	10·8

FIG. 6. Measurements along the valve surface from the umbones to the rugae of *Overtonia fimbriata* (J. de C. Sowerby), (a); and various lamellae on *Avonia* (*Quasiavonia*) *aculeata* (J. Sowerby), (b), that can be identified on both valves in order to compare the relative lengths of pedicle valves and their matching brachial valves.

curved strongly, or geniculated against the pedicle valve to form a common antero-dorsally directed trail.

Internally, the cardinal process developed progressively from its early distinctly bilobed condition (Text-fig. 3). The same basic bilobed pattern can be traced through all the modifications leading to the typical adult cardinal process because of the constraint exercised by the paired muscle bases. Commonly, the cardinal process grew posteriorly, the myophores facing postero-dorsally, and as development proceeded the two lobes became increasingly fused anteriorly by the deposition of secondary shell. At the same time the outer ridges of each myophore curved around the muscle bases to a greater or lesser extent. In this way the outer face of the cardinal process became " folded " to the quadrifid condition, when not medianly fused, or trifid when the two median muscle boundaries had completely fused (Text-fig. 3, d). Further posterior growth and migration of the muscle bases towards the tip of the cardinal process left the base free for the deposition of secondary shell and the formation of a shaft separating the myophores from the base (Text-fig. 3, g). In groups with strongly demarcated ears, ridges developed across their inner margins quite early in life and, with the thickening of the dorsal valve at maturity, commonly fused to the lateral ridges. These ridges continued around the lateral and anterior margins of the visceral disc in some marginiferids.

Brachial ridges became prominent after the development of the visceral region. The outer mantle epithelium deposited secondary shell over the surfaces to which nothing was strongly attached so that the anterior adductor scars usually became strongly outlined while the posterior scars became distinguishable. The median septum was thickened and a ridge commonly developed connecting it to the base of the cardinal process, in so doing usually filling the protegulal cavity, or alveolus (Text-fig. 5, a). The " drag " of the suspended lophophore probably folded the mantle and this led to the development of the strong brachial ridges and the thickenings within the brachial areas of some genera. The pinnate mantle canal system, possibly leaving its trace on the shell in the form of radial ornament, spread anteriorly between the rows of more or less radially arranged tubercles, or between the stronger ridges developed ventrally in some genera, viz. *Eomarginifera* (Pl. 16, fig. 19). Although the radial ornament was developed from the early neanic stages, it became accentuated during growth and this may have been because of the increased development of the mantle canal system. Within genera such as *Avonia* the late development of a radial ornament may be associated with the maturity of gonadal tissue in the mantle canal system. The ridges that developed across the floor of the pedicle valves of certain marginiferids, buxtoniids and dictyoclostids were probably deposited between a pinnate mantle canal system, comparable to that of *Leptagonia analoga*.

Spines are one of the most striking features of the productoids, which together with the chonetoids are the only spinose Strophomenida. Spines are varied in form and probably in function, but developed in similar ways. Where ribbing is present the spines are located close to their crests. It is believed that ribbing in the productoids is commonly associated with the mantle canals and setal follicles at the mantle edge. Spine development probably started at the mantle edge as generative buds of outer

epithelium containing a strand of the mantle canal system which supplied nutrients to the growing tip. Thus, ribbing, spines and mantle canals are probably all associated. It has been recognized for a long time that spines must have contained living tissue, but it was Williams (1956 : 252) who gave the most realistic picture of their growth as " disjunct portions of the tip of the outer epithelium, occupying the ends of the spines and capable of proliferation of secretory cuboidal epithelium independent of the mantle edge ". This concept allows the spine to have grown continually, while the epithelium remained active, and permitted its growth to alter in response to contact with solid objects. This occurred (Pl. 5, figs. 4, 14, 15) by envisaging the shell secretion to have taken place just behind the generative tip of the spine.

By adulthood most spines, except those at the shell margins, had been blocked by shell deposition internally, and had died. However, during growth the spines must have grown rapidly while still close to the valve margins.

In genera such as *Eomarginifera*, with a few major spines that developed only at the onset of adulthood, the spines commonly retain internal connections despite being left well back from the valve margin. These long straight spines most likely acted as stabilizers to the shell after the rotation of the body cavity, relative to the substratum, had ceased.

Throughout adult life some secondary shell deposition took place which accentuated the internal morphology and which possibly continued to modify the cardinal process. Once migration of the muscle bases had ceased, as probably happened after maturity, the muscle scars underwent little change, other than accentuation of outline. The principal anterior and marginal spines retained internal connection and continued to act as stabilizers to the shell until its death. Their internal openings became rimmed and the tubercles increasingly thickened or buried by secondary shell. Extensions and retractions of the anterior mantle margins commonly led to the formation of lamellose frills and thickenings along the margins of the shell.

Eventual death of the brachiopod led to the loss of any active attachment to the substratum, so that the shell became free to be acted upon by sea currents and commonly became a suitable habitat for many epifaunal invertebrates.

IV. SYSTEMATIC DESCRIPTIONS

Superfamily **STROPHALOSIACEA** Schuchert 1913

Family **STROPHALOSIIDAE** Schuchert 1913

Subfamily **STROPHALOSIINAE** Schuchert 1913

EMENDED DIAGNOSIS. Strophalosiidae with no spines on brachial valve.

Genus ***STROPHALOSIA*** King

1844 *Strophalosia* King : 313.
1846 *Strophalasia* King : 28, 92.
1850 *Strophalosia* King : 93 (pars).

EMENDED DIAGNOSIS. Outline subcircular to transversely elliptical with straight hinge-line about two-thirds maximum width, ventral umbo developed but commonly

deformed by cicatrix of attachment; profile gently concavo-convex, adult brachial valve forming short trail; ornament of variably developed lamellae, commonly more prominent on brachial valve, spines restricted to pedicle valve, differentiated into prostrate and more or less erect series; brachial valve spine-free but dimpled; ventral interarea anacline to orthocline, extending full hinge width, delthyrium narrow, triangular, closed by slightly arched pseudodeltidium; dorsal interarea hypercline, shorter and with narrow indistinct chilidium; teeth rounded in outline and oblique to valve margin; cardinal process elongately narrow, quadrifid to trifid but thickened in old-age, supported by posteriorly low median septum and curved socket ridges, indistinct in adulthood; adductor scars slightly raised, smooth, elongately oval and not clearly divided; brachial impressions indistinct, lobate; ventral interior unrecorded.

Type species. *Strophalosia gerardi* King, by subsequent designation of the International Commission on Zoological Nomenclature (1962, Opinion 625).

Discussion. The interpretation of the genus has been controversial from its erection in 1844 owing to the lack of an established type species. In recent years Maxwell (1954), Muir-Wood (1960) and Waterhouse (1964) have discussed the genus and on the application of Muir-Wood the International Commission on Zoological Nomenclature has designated *S. gerardi* King 1846 as type species. While clearly setting out the complex history of the genus, this ruling, unfortunately, includes errors which detract from its validity and *S. gerardi* is so poorly represented in known collections that it remains difficult to give a full description of the genus, based upon the type species.

Within the strophalosiinids considerable weight has been given to the taxonomic importance of the presence or absence of spines on the brachial valve; species with such spines having been assigned to the Strophalosiinae and those without to the Heteralosiinae.

The two type specimens of *S. gerardi* (Pl. 1, figs. 7–9) collected from the Himalayas and kept at University College, Galway, Ireland, have been studied and no trace of spines can be seen on the brachial valves, neither on the external nor internal surfaces, or within the shell structure. This observation has already been made by several authors (e.g. R. H. King 1938, Waterhouse 1964). The external surface of the brachial valve is somewhat lamellose and ornamented by irregular dimples, similar to those commonly seen on *Heteralosia* R. H. King, but neither spine bases nor spines have been found in the adjacent sediment. *Heteralosia* was separated from *Strophalosia* by R. H. King (1938 : 278) to include species " that have a smooth dorsal valve ", and he assigned *S. gerardi* to his new genus believing that *Orthis excavata* Geinitz was the type species of *Strophalosia*. Thus, although common usage has placed species with spinose brachial valves into *Strophalosia*, the ruling of the International Commission necessitates a revision of the Strophalosiidae, including the placing of *Heteralosia* and *Strophalosia* into the same subfamily. A suitable genus must also be found for the spinose species previously assigned to *Strophalosia*.

A study of topotypic specimens of *Heteralosia slocomi* R. H. King (Pl. 1, figs. 1–4), type species of *Heteralosia*, from the Graham formation near Gunsight, Texas, shows

that they are distinct from *S. gerardi*. The Texan shells are about two-thirds the length and width of the Himalayan species and associated with this difference are apparent differences in the spine pattern of the pedicle valves, surface ornamentation and development of the interarea. However, these differences are not so clear in a comparison of the specimens as they would have appeared when both species were of much the same dimensions. For example, the spine bases of both species measure 0·4 mm. in diameter, 10 mm. from the pedicle umbo, and the spine frequency was probably comparable. Unfortunately, it is not possible to compare the internal morphology of the species at similar developmental stages, but the Himalayan brachial interior is comparable to an older developmental stage of the Texan species, assuming normal shell deposition within *H. slocomi*. The stratigraphic position of *S. gerardi* is not known accurately, but is commonly recognized as being Permian. *H. slocomi* comes from the Upper Pennsylvanian of Texas and the genus probably extends into the Permian. The question as to whether *Heteralosia* should be treated as a junior synonym of *Strophalosia* is, therefore, one of opinion regarding size and geographical distribution. The likelihood of obtaining further Himalayan specimens is remote. Congeneric specimens from Tasmania, comparable in all recognizable external features and attributed to " *S. gerardi* " are known from mid-Permian strata. It is to be hoped that more Tasmanian material might assist in the comparison of these genera, but until such a study can be made it is better to retain the two genera, while recognizing their morphological similarities.

One Tasmanian specimen (98216) of " *S. gerardi* " (Pl. 1, figs. 5, 6), in the British Museum (Natural History), has four juvenile shells of from 3·4 to 5·6 mm. wide attached to its pedicle valve. These young shells are transversely elliptical to rectangular in outline and their pedicle valves are in close contact with the adult *Strophalosia*. Spines extend from their pedicle valves, but there is none on the brachial valves.

The brachial valve interior of *S. gerardi*, which accompanies the holotype from the Himalayas, shows a number of informative features. The specimen is partially delaminated and most of the cardinal process has been broken. However, a juvenile stage of development within the cardinal process is exposed, showing it to have been elongately narrow, with slight shoulders on the flanks, anterior to the fused median muscle ridges. This juvenile stage is similar to the cardinal process of *Heteralosia* cf. *fortispinosa* (Pl. 4, fig. 11) from Fermanagh, indicating a point of similarity between these groups. Prominant socket ridges extend at a high angle from the cardinal process base in *S. gerardi*, and these flank the postero-lateral margins of the smooth, slightly raised adductor scars. This contrasts with *Dasyalosia* and *Orthothrix* in which the socket ridges are short, barely reaching the posterior margins of the adductor scars.

More features than that of a spine-free brachial valve link *Strophalosia* and *Heteralosia* and the two genera are here united within the same subfamily, Strophalosiinae Schuchert 1913, which has priority over Heteralosiinae Muir-Wood & Cooper 1960. The strophalosiid genera with spines on both valves (*Crossalosia*, *Dasyalosia*, *Eostrophalosia* and *Orthothrix* of Muir-Wood & Cooper's classification,

1960 : 65) are thus left without a subfamilial status. Of these genera *Dasyalosia* is the best known, and being well represented has been chosen as the type genus of the new subfamily Dasyalosiinae. It may prove necessary to redistribute the genera within these subfamilies, but such a revision is beyond the scope of the present work.

In discussing *Strophalosia*, Muir-Wood (1960 : 316) correctly points out the priority of *Productus spiniferus* Howse and *P. morrisianus* Howse over the respective names *Strophalosia morrisiana* King and *S. spinifera* King. This use of the same specific names by different authors arose because Howse used manuscript names of King that had already been published (*in* Murchison & Verneuil 1845) before King's determinations were made known. Howse's descriptions were published two days before King's and should therefore be accepted. It is unfortunate that Muir-Wood concludes by requesting the suppression of Howse's names in favour of those given by King. (This request was granted by ICZN 1962, opinion 625.) De Koninck (1847 : 263) records his difficulty in comparing his species, *P. lewisianus*, with those of Howse and King because of King's refusal to lend material. It is clear that *S. spinifera* King (= *P. morrisianus* Howse) is synonymous with *P. lewisianus* de Koninck and both came from Humbleton, Durham. *S. morrisiana* King (=*P. spiniferus* Howse) is distinctive in being finely ribbed as well as spinose, but its modern generic position remains to be determined.

Genus ***HETERALOSIA*** R. H. King

Heteralosia cf. ***fortispinosa*** (Hinchey & Ray)

(Pl. 4, figs. 9–19 ; Pl. 5, figs. 1–5)

Description. Outline subrounded, length almost equal to maximum width at midlength of shell ; ventral umbo variable, commonly extending beyond hinge-line which is about three-quarters maximum width, cicatrix of attachment variably developed, ears small, triangular ; profile concavo-convex, depth about two-fifths length ; spines confined to pedicle valve, arranged concentrically and more or less in alternating radial rows of variably disposed erect spines and recumbent spines following shell profile, growth lines on both valves, rarely becoming prominent to lamellose on brachial valve ; ventral interarea apsacline to orthocline with elongate trigonal delthyrium, apically closed by slightly arched pseudodeltidium and filled by dorsal surface of cardinal process ; dorsal interarea much reduced ; teeth small, semi-oval in outline and cross-section, commonly laterally divergent at low angle from hinge-line ; muscle scars poorly defined, apparently lobate and confined posteriorly ; scattered spine openings and row along inside of hinge-line, short sharp tubercles medianly placed ; cardinal process prominent, commonly tapering postero-ventrally, lobes tightly compressed, median myophore ridges narrow on external surface forming bifid distal tip, lateral myophore ridges poorly developed ; socket ridges short, supporting cardinal process, at about 40° to hinge-line but laterally recurring towards it and dying out within about 1 mm.; median septum wide posteriorly at base of cardinal process, extending anteriorly for about one-third adult

valve length, becoming narrow and higher; adductor scars oval, extending about one-half length of septum and variably enclosed postero-laterally by secondary thickening from socket ridges; radially arranged spinose tubercles medianly; shell substance pseudopunctate.

MEASUREMENTS (in mm.)

	length	width
Complete shell (BB.52813)	5·8	9·6
Complete pedicle valve (BB.52814)	7·5	8·7
Complete pedicle valve (BB.52815)	5·0	5·5
Incomplete pedicle valve (BB.52816)	8·5	—
Incomplete brachial valve (BB.52818)	*c.* 5·5	—
Complete brachial valve (BB.52819)	5·5	6·0
Complete brachial valve (BB.52820)	3·0	3·0
Complete pedicle valve (BB.52821)	2·3	2·3
Complete pedicle valve (BB.52822)	2·0	1·8
Complete pedicle valve (BB.52823)	1·4	1·6
Incomplete pedicle valve (BB.52824)	—	*c.* 6·5
Complete pedicle valve, attached (BB.52825)	5·4	6·0
Complete pedicle valve, attached and distorted (BB.52826)	2·7	2·8

LOCALITIES AND HORIZON. Subreefal limestones and shales, Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. *Heteralosia* was previously unrecorded from the British Isles, except for an unnamed species from the Permian near Ripon, Yorkshire, referred to by Muir-Wood & Cooper (1960 : 81). Otherwise, the species assigned by these authors to *Heteralosia* are all from the Mississippian or Pennsylvanian of the American continent. *Heteralosia fortispinosa* (Hinchey & Ray 1935), as illustrated by Muir-Wood & Cooper (1960, pl. 3, figs. 1–5), agrees in known characteristics with the Fermanagh shells, except that the latter are rather smaller in all proportions than those from America. Thus until type material of *H. fortispinosa* can be studied, the Fermanagh shells are identified as *H.* cf. *fortispinosa*.

The species is not strongly curved and peripheral growth of the shell appears to have been isometric. The maximum width is consistently about 10% greater than length. The ventral umbo gives a somewhat rounded outline to the posterior margin, while the hinge-line of the brachial valve is straight; the ears are small on both valves. The postero-ventral surface of the ventral umbo is variably deformed by the cicatrix of attachment, which only rarely is not visible. Usually it is about 1 mm. in diameter and many of the posteriorly placed spines may be deformed distally, where they came into contact with some hard object. In a few instances fragments of shelly material are preserved adhering to the cicatrix, and it is possible to observe the deflection of the spines as they grew into contact with this material (Pl. 5, figs. 4, 15). It is common for such spines to become distorted and somewhat swollen, as if to make a firmer attachment, and this habit indicates that the shell substance of the

spines must have grown behind a slightly protruding bud of outer epithelium. In itself, this bud, was probably of importance in anchorage, and it did allow the growth of the spines to alter in response to contact. The shells show a genetic characteristic which further aided attachment. The alternate rows of more highly angled spines, which appear to have been added during growth by intercalation between dichotomizing rows of the recumbent spines, always grew in a postero-ventral direction, so that as growth continued the more anteriorly placed spines grew back along the shell in an opposite direction to, and only at a slightly higher angle than, the anteriorly directed recumbent spines (Pl. 5, figs. 9, 13). In other words, the constancy of growth direction led to a considerable and progressive alteration in the angle of the spines to the shell surface, and resulted in the maximum contact of spines with the posteriorly placed object of attachment. It is common for the silicified material to have lost most of the more erect, postero-ventrally directed spines, but when they are preserved little of the shell surface can be seen through the dense mat of opposed spines.

The ornament of the brachial valve is irregular, consisting of variably developed, rather dimpled, low rugae, showing a tendency to become anteriorly lamellose. This ornament is most clearly defined at the hinge-line. The dimples probably developed at the valve margin, opposite the spine bases on the pedicle valve, when the valves were in close contact and are uncommon on species with lamellose or spinose brachial valves.

The first formed brachial valve, up to 1 mm. in length, was flat but during subsequent growth the valve became evenly concave, although the degree of curvature was somewhat variable within the species. Internally the median septum is just visible as a thickening at the base of the cardinal process in valves about 2 mm. long, but became clearly differentiated in valves 3 mm. long and extended for one-third of the valve length (Pl. 4, fig. 10). The adult median septum remains low over the posterior one-third of this length, but is narrow and high anteriorly.

The adductor scars are usually visible in valves 3 mm. long, but are not distinct until surrounded by secondary shell at a length of between 5 and 6 mm. Variability in the depth and shape of the ventral umbo appears to have led to some variation in the angle of projection of the cardinal process. Most commonly it grew at an angle of about 130° to the commissural plane, but rarely perpendicular. The distal end of the cardinal process is also rather variable ; the two lobes are always narrowly separated by a groove and the median ridges of each myophore are commonly extended posteriorly. The outer ridges of the myophores are rarely developed, but when present arise one-half to two-thirds the way along the dorsal surface of the cardinal process as subsidiary ridges forming shoulders below its tip. The fused basal portion of the myophore produces a low ridge from the dorsal beak which may be the structure called a lophidium by Muir-Wood & Cooper (1960 : 6).

The ventral muscle field is too poorly differentiated to be distinguishable through a growth series. The teeth show no proportional alteration, but in adult valves it is possible to distinguish the overgrowth of the interarea onto their posterior margins, a process which differentiated the teeth more fully from the interarea during growth.

A row of spines close to the ventral hinge-line commonly retained internal con-

nections below the interarea, otherwise the remaining spines only sporadically retained internal openings, and these appear to bear relationship neither with the spines making anchorage to a foreign object, nor to those that grew in a particular direction, i.e. either the erect or recumbent spines.

TABLE 1

$\overline{\mathrm{L}}$ mm. (var.) = 4·08 (3·709)	$\overline{\mathrm{L}}$ mm. (var.) = 4·08 (3·709)
$\overline{\mathrm{W}}$ mm. (var.) = 4·30 (4·431)	$\overline{\mathrm{DelH}}$ mm. (var.) = 0·38 (0·040)
r = 0·974	r = 0·941
a (var.) = 1·093 (0·00175)	a (var.) = 0·108 (0·000037)
$\overline{\mathrm{W}}$ mm. (var.) = 4·30 (4·431)	$\overline{\mathrm{DelH}}$ mm. (var.) = 0·38 (0·040)
$\overline{\mathrm{HiW}}$ mm. (var.) = 2·93 (2·645)	$\overline{\mathrm{DelW}}$ mm. (var.) = 0·28 (0·012)
r = 0·965	r = 0·836
a (var.) = 0·773 (0·00117)	a (var.) = 0·54 (0·0026)

TABLE 1. Statistics for length (L), maximum width (W), width of hinge-line (HiW), height of delthyrium (DelH), and the width of the delthyrium (DelW) at the hinge-line of 37 pedicle valves of *Heteralosia* cf. *fortispinosa* (Hinchey & Ray).

TABLE 2

$\overline{\mathrm{L}}$ mm. (var.) = 3·52 (1·703)	$\overline{\mathrm{L}}$ mm. (var.) = 3·52 (1·703)
$\overline{\mathrm{W}}$ mm. (var.) = 3·94 (2·396)	$\overline{\mathrm{MsL}}$ mm. (var.) = 1·09 (0·346)
r = 0·968	r = 0·729
a (var.) = 1·186 (0·00638)	a (var.) = 0·451 (0·00793)
$\overline{\mathrm{W}}$ mm. (var.) = 3·94 (2·396)	$\overline{\mathrm{L}}$ mm. (var.) = 3·52 (1·703)
$\overline{\mathrm{HiW}}$ mm. (var.) = 3·08 (1·734)	$\overline{\mathrm{CpL}}$ mm. (var.) = 0·36 (0·053)
r = 0·969	r = 0·853
a (var.) = 0·851 (0·00368)	a (var.) = 0·170 (0·00070)

TABLE 2. Statistics of length (L), maximum width (W), width of hinge-line (HiW), length of cardinal process, from its base (CpL), and length of the median septum from the same point (MsL) of 14 brachial valves of *Heteralosia* cf. *fortispinosa* (Hinchey & Ray).

Subfamily **DASYALOSIINAE** nov.

DIAGNOSIS. Strophalasiidae with spines on both valves.

Genus ***DASYALOSIA*** Muir-Wood & Cooper 1960 : 76

TYPE SPECIES. *Spondylus goldfussi* Muenster 1839, by original designation of Muir-Wood & Cooper (1960).

Dasyalosia goldfussi (Muenster) was described from the Zechstein of Gara, Germany, and the genus was described by Muir-Wood & Cooper (1960). These authors are incorrect in describing the cardinal process as " not having a lobate myophore ". The dorsal interior figured by them (1960, pl. 6, figs. 16, 17) has a broken cardinal

process, as can be seen from conspecific material, also from Gara, in the British Museum (Natural History) (B.73242 and B.73246). From these specimens it is clear that the cardinal process extends well beyond the hinge-line and expands distally so that it can be easily broken close to the hinge-line. The cardinal process of *D. lamnula* (Pl. 3, figs. 8, 9) is closely comparable to that of the German type specimens.

The Fermanagh species not only have similar cardinalia to *D. goldfussi*, but externally they are alike in ornamentation ; both have pedicle valves thickly covered by spines that grew in two sets, those growing posteriorly commonly clasping an object such as a productid spine or bryozoan stalk. No clear evidence of actual cementation of the ventral umbo or of a pedicle sheath have been found, but the umbo is commonly flattened against a piece of shell debris. The juvenile clasping spines probably assisted in the fixation of the young shells. The spine pattern of *D. goldfussi* is similar to that of *D. panicula*, with its preponderance of erect, posteriorly curving spines. They are also similar in having ventral interareas that extend the full widths of their hinge-lines and their brachial valves are more lamellose than their pedicle valves. It is likely that the Carboniferous species was ancestral to the Permian German species.

Both the Irish species are more lamellose than *D. goldfussi* ; their erect spines apparently never extended posteriorly to quite the same extent and the valves did not reach the same size as specimens from Germany. The concavity of brachial valves of *Dasyalosia* results from its geniculation against the pedicle valve margin in adulthood, when an increase in the thickness of the body-cavity ceased. Young valves are more plano-convex in profile and the visceral disc is but slightly curved.

At present, only the type species and those species here described from Co. Fermanagh are assigned to the genus.

Dasyalosia panicula sp. n.

(Pl. 2, figs. 1–17 ; Pl. 3, figs. 1–5)

Diagnosis. Outline subrounded to rounded trigonal, length about equal to maximum width, hinge-line straight, nearly one-half maximum width ; umbo pointed, extending beyond hinge-line, rarely with cicatrix of attachment or distorted ; profile plano-convex to slightly concavo-convex, about one-third as thick as long ; concentric ornament of sublamellose ridges from which arise spines of two series in radially arranged rows ; primary and intercalated rows of anteriorly directed recumbent spines alternate with dichotomizing rows of postero-ventrally directed spines which are commonly grouped into threes and widen distally ; brachial valve similar, but erect spines not grouped ; ventral interarea prominent, concave and orthocline, extending full width of hinge-line ; delthyrium narrow, triangular, covered by flat pseudodeltidium ; dorsal interarea reduced, about one-quarter length of ventral interarea ; teeth prominent, semioval in outline, concave dorsally and commonly diverging at about 25° from hinge-line ; adductor scars prominent, upon elongately trigonal platforms separated by median groove, extending about one-third valve

length ; diductor scars indistinct, rounded and flanking ; fine spine-like tubercles developed medianly ; spines retain internal openings marginally ; cardinal process laterally compressed, elongate and extending postero-ventrally, median myophore ridges extended and narrowly separated ; commonly broad groove on internal face of cardinal process, laterally enclosed by median ends of supporting socket ridges at about 35° from hinge-line ; sockets deep, externally enclosed by interarea ; adductor scars subrounded to elongately oval, raised and extended anteriorly as tuberculate ridges ; adult median septum about three-fifths valve length, low and broad posteriorly, becoming narrow and prominent anteriorly ; slight lateral ridges across inside of much reduced ears ; spine openings marginal ; tubercles medianly and anteriorly placed, shell substance pseudopunctate.

MEASUREMENTS (in mm.)		length	width
HOLOTYPE.	Complete shell (BB.52790)	10·3	10·5
PARATYPES.	Pedicle valve (BB.52791)	*c.* 8·0	8·2
	Incomplete pedicle valve (BB.52792)	*c.* 7·6	7·9
	Complete pedicle valve (BB.52793)	3·1	3·2
	Complete brachial valve (BB.52794)	6·0	6·2
	Complete brachial valve (BB.52795)	3·4	3·9
	Complete shell (BB.52796)	4·1	4·3
	Pedicle valve attached to bryozoan (BB.52797)	4·0	3·5
	Incomplete pedicle valve on bryozoan (BB.52798)	4·5	—
	Pedicle valve showing spine growth-lines (BB.52799)	4·0	4·3
	Pedicle valve (BB.52800)	8·0	*c.* 8·4
	Complete pedicle valve on bryozoan (BB.52920)	4·0	4·3

LOCALITIES AND HORIZON. Subreefal limestones and shales at Carrick Lough, and sporadically at Bunnahone, about 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

Dasyalosia lamnula sp. n.

(Pl. 3, figs. 6–18 ; Pl. 4, figs. 1–8 ; Text-fig. 7)

DIAGNOSIS. Outline subcircular, length approximately equal to maximum width occurring at mid-length ; hinge-line straight, about two-thirds maximum width ; profile plano-convex to slightly concavo-convex, ventral umbo commonly rounded

and extending slightly beyond hinge-line ; about one-third as thick as long ; ventral beak rarely with cicatrix of attachment, rarely distorted ; concentric ornament of prominent lamellose ridges on both valves ; spines coarse, about 0·2 mm. in diameter on ventral valve, arranged in two series of alternating radial rows arising from concentric ridges, one set about normal to shell with rows added by intercalation, other set anteriorly directed, nearly parallel to shell surface, and branching dichotomously ; brachial valve with finer anteriorly directed spines increasing in number anteriorly, and few at high angle and incurving on cardinal extremities ; ventral interarea variably developed, short and confined umbonally, orthocline ; pseudodeltidium flat, partially filling narrow triangular delthyrium ; dorsal interarea much reduced or lacking ; teeth semioval in outline, about as wide as long, diverge from interarea and more or less curved ; adductor scars elongately oval to trigonal, on raised elongate rectangular platform, three-fifths as wide as long and one-quarter valve length, with shallow median groove ; diductor scars indistinct, spreading antero-laterally from adductor scars ; internal spine openings few ; cardinal process bilobed, posteriorly elongate and medianly fused except at distal tip ; myophores postero-dorsally directed, deeply grooved and extending towards dorsal base of cardinal process ; groove between fused lobes extends to ventral base ; short socket ridges at about 50° to mid-line anteriorly enclose short deep sockets, closely flanking cardinal process ; adult valves with ridges at low angle to hinge-line around inside of small ears to antero-lateral margin ; adult median septum one-half to two-thirds valve length, low and supporting cardinal process posteriorly, high and narrow anteriorly ; adductor scars raised, rounded to trigonal, about one-fifth valve length ; shell substance pseudopunctate.

		length	width (mm.)
Holotype.	Complete shell (BB.52801)	6·5	6·9
Paratypes.	Incomplete pedicle valve (BB.52802)	c. 15·0	17·0
	Complete pedicle valve (BB.52803)	8·5	10·0
	Incomplete pedicle valve (BB.52804)	4·5	c. 4·0
	Incomplete pedicle valve (BB.52805)	4·4	—
	Complete brachial valve (BB.52806)	9·0	10·5
	Complete brachial valve (BB.52807)	3·6	4·3
	Complete brachial valve (BB.52808)	2·2	2·6
	Incomplete brachial valve showing the cardinalia (BB.52809)	—	—
	Incomplete brachial valve (BB.52810)	—	—
	Complete pedicle valve (BB.52811)	2·2	2·1
	Complete pedicle valve (BB.52812)	1·3	1·3

Localities and horizon. Subreefal limestones and shales, Bunnahone and sparsely at Carrick Lough, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

Discussion. The Fermanagh species show little alteration in the proportions of outline during growth, the coefficients of correlation for both length and width, and

length and thickness are high (Tables 3, 5) indicating a regular marginal accretion to the shell. The persistence of the allometric relationship between paired parameters in *D. lamnula*, is probably a reflection of the greater curvature of its pedicle valve, and contrasts with the apparently isometric growth of *D. panicula*. It may be that larger samples of *D. panicula* would prove to be allometric.

The ventral interarea of *D. lamnula* is narrowly confined to the umbonal region and does not extend beyond a hinge-line width of about 2·0 mm. This gives the umbonal slopes a high angle and led to the formation of flattened ears. The hinge-line width of these shells is about two-thirds of the maximum width, while the adult interarea is only one-fifth, or less, of the maximum width. This is in sharp contrast to the fully developed interarea of *D. panicula*, which extends to the cardinal extremities.

A feature confined to *D. lamnula*, is the rare slight sulcation seen in the antero-median halves of 5 out of 36 pedicle valves.

The ventral elongate and raised adductor scars are developed in shells only 3 mm. long (Pl. 4, fig. 5) and can rarely be distinguished as a pair of oval elevations, just anterior to the socket ridges, in valves only 2 mm. long. Statistical comparisons of the lengths of the adductor scars compared to the full widths of the adductor fields of either valve show that they have low coefficients of correlation, indicating that their growth was not regular within the sample. Because the correlation coefficient

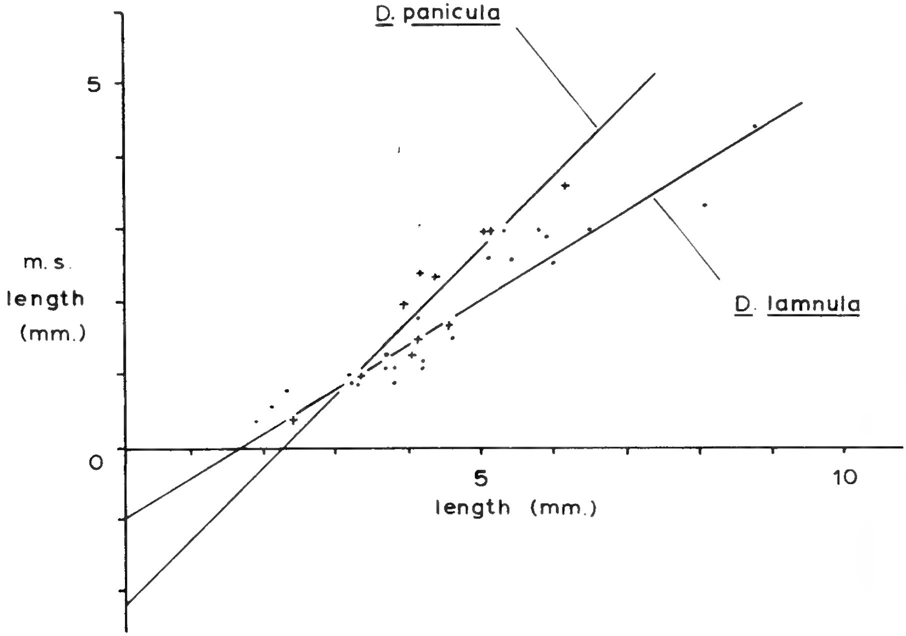

FIG. 7. Plots of the paired measurements of total length of the brachial valve (length) against the length of the median septum (m.s. length) for *Dasyalosia panicula* sp. n. (+), and *D. lamnula* sp. n. (.), illustrating the different growth axes of characteristics for the species.

is not significant ($P > 0{\cdot}01$), the axes of growth for the adductor scars have not been set out in the tables. The dorsal median septum is first seen in shells between 3 and 4 mm. long (Pl. 2, fig. 8). In comparing the brachial valve length with the full length of the median septum, as measured from the hinge-line, a high correlation is obtained. Although the mean length of the median septum is less than half that of the valve, the growth axes, " a", are between 0·62 and 1·00. However, the intersects of these growth axes with the septal length axes are between — 1·0 and — 2·0, so that in both species the start of growth of the median septum might be expected when the valve was about 2 mm. long (Text-fig. 7). The median septum arose between the adductor scars and at the base of the cardinal process and in valves about 6 mm. long grew highest along its anterior margin. In adult shells it was always prominent anteriorly and extended beyond the adductor scars for a little more than one-half the adult valve length (Pl. 4, fig. 2). The median septum appears to differ somewhat in *D. panicula*, in that it grew to about three-fifths of the valve length and arose about 1·5 mm. in front of the cardinal process at a valve length of about 4 mm. Brachial ridges are not distinguishable in either species.

Spines are abundant on each valve of the two species, and arose from the posterior part of each concentric lamellose ridge (Pl. 3, fig. 15). This fixed their position at certain growth stages and they are further located by being radially arranged, a feature seen more readily on pedicle valves than brachial valves because of the alternation, on the former, of erect spines with low angled, or recumbent spines. The spines clearly reached considerable lengths ; a young pedicle valve 2 mm. long has spines of the same length still preserved, while adult shells have broken spines up to 5 mm. long. The differentiation into two sets of spines is primary, being recognized on valves of less than 1·5 mm. long (Pl. 4, figs. 3, 4). Both sets are initially of the same diameter at any growth stage. The erect spines are first anteriorly directed but then curve normal to the shell surface or are postero-ventrally directed. Around the umbo these spines are medianly incurved in a clasping fashion. The alternating recumbent spines arose initially like the erect ones but immediately bent anteriorly to lie more or less parallel to the valve surface and with growth overlap and the more anteriorly placed spines of their row (Pl. 2, fig. 17). A lateral increase in the number of rows of spines was achieved by a diagnostically important pattern of branching and intercalation. In *D. lamnula*, the erect spines form primary and intercalated rows between the recumbent spine rows which bifurcated at each additional intercalation, these occurred at approximately the same growth stage for any one specimen. This contrasts with *D. panicula* in which the arrangement of spines is of primary and intercalated rows of recumbent spines between bifurcating rows of erect spines. Moreover, beyond a pedicle valve length of about 2 mm. the radial rows of erect spines sporadically divided giving groups of three or five spines as prominent tufts, a feature recorded in the specific name. These spines are commonly expanded towards their distal ends and are occasionally somewhat laterally flattened, as if in response to contact with a hard surface (Pl. 2, fig. 9). Such a grouping of three or more erect spines commonly occurred prior to the division of the row as a whole, with the anterior intercalation of a row of recumbent spines. There is a tendency

for these erect spines to recurve posteriorly rather more than is usual in *D. lamnula*. The distal ends of the erect spines of *D. lamnula* are never splayed or sharply bent, and thus probably did not come into contact with any solid foreign body, as did those of *D. panicula*. The external ornamentation of the brachial valve of the two species is similar, both having anteriorly directed spines at a low angle to the valve surface, which are of a narrower diameter than those of the pedicle valves. However, erect spines are scattered rather sporadically over the surfaces and concentrated upon the cardinal extremities, especially on the better developed "ears" of *D. lamnula*, where they curve antero-medianly to overhang much of the valve. The dorsal erect spines of *D. panicula* are perhaps more numerous antero-medianly, tend to curve posteriorly and are expanded in a similar way to those of the pedicle valve. Fine growth lines can be seen on the valves and encircling the spines. The most distinctive features which differentiate *D. lamnula* from *D. panicula*, are their spine arrangements, the widths of their ventral interareas and hinge-lines compared to their maximum widths, and the difference of concentric ornamentation. Less distinct differences occur in their dorsal median septa, adductor scars, sulcation of the pedicle valve and deformation of the ventral umbones.

The concentric ridges, from which the spines arose, have prominent lamellose extensions in *D. lamnula*, whilst remaining only incipiently lamellose in *D. panicula*.

Unlike *D. lamnula*, the ventral umbo of *D. panicula* is commonly flattened or distorted by a cicatrix of attachment, or by the presence of some skeletal debris. Several specimens have fragments of bryozoan colonies adhering to their umbones and the posterior erect spines can be seen to cling around these fenistellid stems (Pl. 3, figs. 1–5). Spines curve and cling to such material from a distance of 1·5 mm. Rarely the posterior part of a pedicle valve is dented as a result of its growth around some foreign object and the surrounding spines can be seen to have grown over this material.

Although the slope of the growth axis "a" for length and width, shows no significant difference ($P > 0{\cdot}05$) between the species, *D. lamnula* does seem to have grown larger than *D. panicula* (i.e. *D. lamnula* commonly attained a length of about 15 mm., while *D. panicula* is seldom seen longer than 10 mm. Tables 3 and 5 suggest the converse because of the tendency for large specimens of *D. lamnula* to have been broken). The two are significantly different ($P < 0{\cdot}05$) in regard to their widths of hinge-line compared with their maximum widths ; *D. panicula* having a significantly narrower hinge width. A further important difference is that the ventral interarea extends for almost the full width of the hinge-line, while being confined to the narrow umbonal region of *D. lamnula*. This persistence of the interarea led to the formation of gentle umbonal slopes so that the ventral umbo and ears are less well defined than in *D. lamnula*.

The adductor scars of both species are similarly placed and have comparable outlines, but those of *D. panicula* appear to be less well differentiated and less raised, while the ventral scars of this species do not show the slight ridges seen extending from the antero-lateral corners of the scars of *D. lamnula*. These ridges may mark

the trunks of the *vascula media*. The fine spine-like tubercles in the mid regions of *D. panicula* are not so well developed in *D. lamnula*.

From a careful study of the exteriors of these species one might be tempted to consider the differences great enough to warrant generic recognition. This is particularly so in consideration of the differences in the development of the interareas and the different patterns of spine arrangement. However, the similarities of the interiors are such as to indicate a close relationship and one which, in the writer's opinion, does not allow such a division, although it is clear that the two form distinct species groups.

TABLE 3

$$\begin{aligned} \overline{L}\ \text{mm. (var.)} &= 5{\cdot}49\ (4{\cdot}139) \\ \overline{W}\ \text{mm. (var.)} &= 5{\cdot}57\ (4{\cdot}459) \\ r &= 0{\cdot}941 \\ a\ \text{(var.)} &= 1{\cdot}037\ (0{\cdot}0069) \end{aligned}$$

$$\begin{aligned} \overline{L}\ \text{mm. (var.)} &= 5{\cdot}49\ (4{\cdot}139) \\ \overline{Th}\ \text{mm. (var.)} &= 1{\cdot}52\ (0{\cdot}389) \\ r &= 0{\cdot}952 \\ a\ \text{(var.)} &= 0{\cdot}306\ (0{\cdot}00048) \end{aligned}$$

$$\begin{aligned} \overline{W}\ \text{mm. (var.)} &= 5{\cdot}57\ (4{\cdot}459) \\ \overline{HiW}\ \text{mm. (var.)} &= 3{\cdot}04\ (1{\cdot}040) \\ r &= 0{\cdot}973 \\ a\ \text{(var.)} &= 0{\cdot}483\ (0{\cdot}00065) \\ r_e &= 0{\cdot}987 \\ \alpha\ \text{(var.)} &= 0{\cdot}891\ (0{\cdot}00111) \end{aligned}$$

TABLE 3. Statistics of length (L), maximum width (W), thickness (Th) and width of the hinge-line (HiW) of 20 pedicle valves of *Dasyalosia panicula* sp. n.

TABLE 4

$$\begin{aligned} \overline{L}\ \text{mm. (var.)} &= 4{\cdot}25\ (0{\cdot}917) \\ \overline{W}\ \text{mm. (var.)} &= 4{\cdot}76\ (1{\cdot}098) \\ r &= 0{\cdot}945 \\ a\ \text{(var.)} &= 1{\cdot}091\ (0{\cdot}01423) \end{aligned}$$

$$\begin{aligned} \overline{L}\ \text{mm. (var.)} &= 4{\cdot}25\ (0{\cdot}917) \\ \overline{SpL}\ \text{mm. (var.)} &= 2{\cdot}03\ (0{\cdot}926) \\ r &= 0{\cdot}750 \\ a\ \text{(var.)} &= 1{\cdot}005\ (c{\cdot}0490) \end{aligned}$$

TABLE 4. Statistics of length (L), maximum width (W) and length of median septum from the hinge-line (SpL) in 11 brachial valves of *Dasyalosia panicula* sp. n.

TABLE 5

$$\begin{aligned} \overline{L}\ \text{mm. (var.)} &= 3{\cdot}96\ (3{\cdot}030) \\ \overline{W}\ \text{mm. (var.)} &= 4{\cdot}04\ (3{\cdot}956) \\ r &= 0{\cdot}987 \\ \text{Log}_e\ \overline{L}\ (\text{var. log}_e\ L) &= 1{\cdot}287\ (0{\cdot}1774) \\ \text{Log}_e\ \overline{W}\ (\text{var. log}_e\ W) &= 1{\cdot}2925\ (0{\cdot}2175) \\ r_e &= 0{\cdot}987 \\ \alpha\ \text{(var.)} &= 0{\cdot}903\ (0{\cdot}00089) \end{aligned}$$

$$\begin{aligned} \overline{L}\ \text{mm. (var.)} &= 3{\cdot}96\ (3{\cdot}030) \\ \overline{Th}\ \text{mm. (var.)} &= 1{\cdot}29\ (0{\cdot}511) \\ r &= 0{\cdot}952 \\ \text{Log}_e\ \overline{L}\ (\text{var. log}_e\ L) &= 1{\cdot}287\ (0{\cdot}1774) \\ \text{Log}_e\ \overline{Th}\ (\text{var. log}_e\ Th) &= 0{\cdot}1228\ (0{\cdot}2669) \\ r_e &= 0{\cdot}959 \\ \alpha\ \text{(var.)} &= 1{\cdot}2267\ (0{\cdot}00524) \end{aligned}$$

TABLE V—*contd.*

$\overline{W}$ mm. (var.) = 4·04 (3·956)	$\bar{L}$ mm. (var.) = 3·96 (3·030)
$\overline{HiW}$ mm. (var.) = 2·48 (2·156)	$\overline{AdL}$ mm. (var.) = 0·996 (0·828)
r = 0·933	r = 0·501
$\mathrm{Log_e}\,\overline{W}$ (var. $\log_e W$) = 1·2925 (0·1774)	$\mathrm{Log_e}\,\bar{L}$ (var. $\log_e L$) = 1·287 (0·1774)
$\mathrm{Log_e}\,\overline{HiW}$ (var. $\log_e$ HiW) = 0·7602 (0·2995)	$\mathrm{Log_e}\,\overline{AdL}$ (var. $\log_e$ AdL) = 0·2995 (0·6070)
r_e = 0·943	r_e = 0·559
α (var.) = 1·174 (0·00664)	α (var.) = 0·586 (0·01026)

$\overline{AdL}$ mm. (var.) = 0·996 (0·828)
$\overline{AdW}$ mm. (var.) = 0·636 (0·076)
r = 0·419

TABLE 5. Statistics of length (L), maximum width (W), thickness (Th), width of hinge-line (HiW), length of adductor scars (AdL) and width of adductor field (AdW) of 25 pedicle valves of *Dasyalosia lamnula* sp. n.

TABLE 6

$\bar{L}$ mm. (var.) = 4·42 (3·024)	$\bar{L}$ mm. (var.) = 4·42 (3·024)
$\overline{W}$ mm. (var.) = 4·91 (4·000)	$\overline{SpL}$ mm. (var.) = 1·78 (1·163)
r = 0·970	r = 0·949
a (var.) = 1·1502 (0·00344)	a (var.) = 0·620 (0·00173)
$\overline{W}$ mm. (var.) = 4·91 (4.000)	$\overline{W}$ mm. (var.) = 4·91 (4·000)
$\overline{HiW}$ mm. (var.) = 3·20 (2·287)	$\overline{AdW}$ mm. (var.) = 0·51 (0·054)
r = 0·956	r = 0·907
a (var.) = 0·756 (0·00224)	a (var.) = 0·116 (0·00011)

$\overline{AdL}$ mm. (var.) = 0·89 (0·164)
$\overline{AdW}$ mm. (var.) = 0·51 (0·054)
r = 0·459

TABLE 6. Statistics of length (L), maximum width (W), width of hinge-line (HiW), length of median septum from the hinge-line (SpL), and length (AdL) and widths (AdW) of the adductor field in 24 brachial valves of *Dasyalosia lamnula* sp. n.

Family **LEIOPRODUCTIDAE** Muir-Wood & Cooper 1960

Subfamily **LEIOPRODUCTINAE** Muir-Wood & Cooper 1960

Genus ***ACANTHOPLECTA*** Muir-Wood & Cooper 1960

EMENDED DIAGNOSIS. Outline subquadrate, hinge-line straight, commonly widest part of shell, umbo rounded extending slightly beyond hinge-line ; profile deeply concavo-convex, not geniculate, body cavity moderately deep ; ventro-anterior fold in slight median sulcus of pedicle valve corresponding to sulcation of

brachial valve ; anteriorly directed furrow at valve margin ; radial ornament lacking, concentric rugae poorly defined, low rounded and irregular across about one-half of pedicle valve and brachial valve visceral disc ; growth-lines distinct ; spines commonly confined to pedicle valve, in double row close to hinge-line, sparsely scattered with rough quincuncial arrangement on rugae and over smooth venter, and with low plications extending anteriorly from their bases ; ventral adductor scars poorly differentiated from flanking diductor scars, separated medianly by low median ridge, muscle field finely ridged longitudinally ; hinge-line thickened by angular ridge ; dorsal valve with low broad cardinal process, two lobes fused and raised medianly ; lateral ridges strong, continuing along hinge-line to postero-lateral margins ; adductor scars raised, divisible into elongately trigonal anterior and narrower posterior scars ; median septum low posteriorly, high and blade-like anteriorly ; brachial impressions obscure, elongately lobate, at high angle to mid-line.

TYPE SPECIES. *Producta mesoloba* Phillips 1836, by original designation of Muir-Wood & Cooper (1960 : 170).

DISCUSSION. Emendation of the original diagnosis of Muir-Wood & Cooper (1960 : 170) mainly concerns the brachial valve, which appears to have been described from immature specimens, and which, judging by the present material is very rarely, if ever spinose. An examination of specimen B.13000 (Muir-Wood & Cooper 1960 pl. 44, figs. 10–14) failed to show dorsal spines. The dorsal interior is discussed more fully under the discussion of *A. mesoloba* below. Muir-Wood & Cooper (1960 : 171) state that geniculation occurs in both valves. However, their figure (pl. 44, fig. 13) fails to show this, as do those of Davidson (1861, pl. 31, figs. 6, 9) and Thomas (1914, pl. 20, fig. 21), and the present material. The brachial valve is certainly regularly concave until the furrow at its anterior margin is reached. This concavity is more regular than that of *Plicatifera*. The genus is readily distinguished from *Plicatifera* by its more rounded profile, irregular, low rounded rugae, double row of spines close to the hinge-line, its antero-median fold and distinctive interior.

Acanthoplecta mesoloba (Phillips)

(Pls. 5, figs. 16–22 ; Pl. 6, figs. 1–5)

1836 *Producta mesoloba* Phillips : 215, pl. 7, figs. 12, 13.
1914 *Pustula mesoloba* (Phillips) Thomas : 327, pl. 20, figs. 18–21.
1960 *Acanthoplecta mesoloba* (Phillips) Muir-Wood & Cooper : 170, pl. 44, figs. 10–17.

EMENDED DIAGNOSIS. Subquadrate to subrounded, commonly with prominent ears and hinge-line widest part of shell, length about three-fifths width ; evenly but strongly concavo-convex with moderate body cavity and thickness about three-quarters length, umbo low with gentle slopes ; median fold in shallow sulcus and corresponding fold of brachial valve, to anterior margin from about middle of rugate posterior region ; anterior margins of valves folded antero-ventrally forming transverse furrow ; about 18 to 20 low indistinct rugae developed posteriorly on pedicle

valves and complete visceral region of brachial valves; growth lines prominent; stout spines almost entirely confined to pedicle valve, suberect from rugae and variably placed in rough quincuncial pattern; anterior spines and those close to hinge-line retain internal openings; ventral muscle scars poorly differentiated, ribbed, about one-half length of visceral region; cardinal process broad and sessile, myophores deeply incised, dorso-posteriorly directed with fused median muscle boundaries; lateral ridges narrowly divergent from hinge-line in young, but strongly developed along hinge-line in adult, medianly form strong posteriorly directed articulatory platforms at sides of cardinal process; adductor scars raised, about two-fifths length of visceral disc and about five-sixths as wide as long, divisible into anterior and posterior scars; median septum from between adductor scars to about one-half valve length, narrow and high anteriorly; brachial impressions poorly defined, posterior margins at about 75° to mid-line, lobate and extending towards lateral margins; anterior regions and trail tuberculate.

MEASUREMENTS (in mm.)

	length	width
Brachial valve (BB.52829)	9·0	c. 13·0
Incomplete brachial valve (BB.52831)	20·0	c. 33·0

DISCUSSION. Specimens are not prolific or well preserved in the Fermanagh fauna so that recourse to previous descriptions and illustrations is necessary to supplement the diagnosis given here.

Muir-Wood & Cooper (1960 : 171) assigned only *A. mesoloba* to their genus and their description of the dorsal interior appears to have been based upon a specimen (possibly pl. 44, fig. 17) which does not show fully developed characteristics (cf. Pl. 5, figs. 20, 21). Development of the dorsal interior was such that in young valves, less than 10 mm. long, the cardinal process was still distinctly bilobed, the lateral ridges were only about one-third of the hinge-line width, and diverged from it at about 15°, the adductor scars and median septum were scarcely distinguishable (Pl. 5, fig. 17). During growth the cardinal process became wider and, as the median muscle boundary ridges of each myophore fused together, overhung a distinct alveolus; the lateral ridges became increasingly thickened medianly and extended towards the cardinal extremities and the median septum developed, mainly anterior to the ill-defined and longitudinally ridged adductor scars. It was only after attaining approximately maximum dimensions, viz. over about 20 mm. long and about 34 mm. wide, that secondary shell was deposited anterior to the cardinal process, so filling the alveolus, that the raised adductor scars developed and became clearly divisible into anterior and posterior scars, and that the lateral ridges had fully thickened along the hinge-line and formed the strong articulatory surfaces on either side of the myophores of the cardinal process (Pl. 6, fig. 2). At this growth stage also, the brachial impressions started to become visible.

Previous authors have been rather vague about the spinose nature of the brachial valve, although Muir-Wood & Cooper (1960 : 171) correctly describe it as having

"few spines". The presence of scattered dimples between some of the rugae may be confused for spine bases, but two brachial valves in seven incomplete Fermanagh specimens do show the bases of one spine each.

Genus *PLICATIFERA* Chao 1927

1927 *Plicatifera* Chao : 25.
1928 *Plicatifera* Chao ; Chao : 61.
1960 *Plicatifera* Chao ; Muir-Wood & Cooper : 201, pl. 50, figs. 13–23.

TYPE SPECIES. *Productus plicatilis* J. de C. Sowerby 1824, by original designation of Chao (1927 : 25).

DISCUSSION. The genus was redefined and its taxonomic position established by Muir-Wood & Cooper (1960 : 201). The diagnosis of these authors differs from the specific diagnosis given here in not mentioning radial ornamentation and by the absence of dorsal spines. The nature of radial ornamentation has been discussed at length by Thomas (1914 : 333) who concluded that its presence was entirely the result of local "decortication" of the shell. The writer's experience is that both pedicle and brachial valves, show a ribbing beyond a length of about 5 mm. and to a point about mid-way between the last ruga and the anterior margin. This is true not only on the Fermanagh shells but on the type specimen figured by Sowerby (1824, pl. 459, fig. 2), B.M.(N.H.) No. 60960. The ribbing is best seen where it crosses the anterior rugae, but also in the interrugal spaces, where it forms an indistinct reticulation, and immediately anterior of the rugae, close to the point of "geniculation" of the pedicle valve (Pl. 6, fig. 7). On *P. plicatilis* ribbing occurs with a frequency of 8, 9 and 10 ribs per 5 mm. width on 3, 3 and 2 pedicle valves just anterior of the last ruga. They are similarly developed on brachial valves. Exfoliation of the brachiopod shell exposes younger shell substance, commonly deposited in a similar way to deposition at the growth margin at that particular stage, or mimicking the surface immediately covering that area, according to the depth of exfoliation. Thus ribbing seen on an exfoliated surface, as admitted by Thomas (1914 : 333) might be expected to show at the surface, either at that place, or more anteriorly. As the present material is silicified, it is impossible to be dogmatic about the occurrence of exfoliation, however, it is unlikely to have occurred as spines are commonly retained and the rugae well formed and sharp. It is unlikely that abrasion occurred in the interrugal spaces, or deep within the concavity of the shell, at the point of the brachial valve geniculation ; places where ribbing can be well seen. For these reasons it is believed that the ribbing was developed primarily, at the shell margins during the greater part of growth, and that it is of diagnostic importance.

The brachial impressions are described for the first time. In *P. plicatilis* they are lobate, extending antero-laterally from between the anterior and posterior adductor scars at about 60° to the mid-line, and extending almost to the antero-lateral corners of the visceral disc. They extend about two-thirds of the valve length and about one-half of their own greatest width (Pl. 6, fig. 15). The enclosing ridges are low and broad, are best seen posteriorly, and the rugation within the areas enclosed is somewhat blurred.

Plicatifera plicatilis (J. de C. Sowerby)

(Pl. 6, figs. 6–15 ; Pl. 7, figs. 1–18 ; Text-fig. 8)

1824 *Producta plicatilis* J. de C. Sowerby : 85, pl. 459, fig. 2.
1914 *Pustula plicatilis* (J. de C. Sowerby) Thomas : 331, pl. 20, fig. 22.
1927 *Plicatifera plicatilis* (J. de C. Sowerby) Chao : 25.
1928 *Productus pseudoplicatilis* Muir-Wood : 189, pl. 11, figs. 17*a–e*.

EMENDED DIAGNOSIS. Subrectangular, length about one-half maximum width, at or equal to width of hinge-line, ears broadly convex, umbonal slopes gentle ; profile unequi-concavo-convex to plano-convex, curvature slight over rugate regions ; pedicle valve gently geniculated with long curved and slightly sulcate venter and trail ; thickness about equal to length, body cavity deep ; radial ornament forming slight, uneven reticulation with stronger rugae, and continuing beyond on to non-rugate region ; about 9 ribs in 5 mm. width, anterior of rugae ; about 24 prominent and regular rugae cover one-half pedicle valve length and whole brachial valve, except trail ; growth lines distinct on smooth venter and prominent on trail ; spines sparsely developed but strong ; clasping spines and pedicle sheath on juvenile valves, adult pedicle valves with about six ill-defined radial rows of 2 or 3 spines set on rugae, rows continued on lateral and antero-lateral smooth flanks ; ventral adductor field nearly one-half valve length and two-fifths as wide as long ; diductor scars extending slightly beyond adductor scars ; cardinal process distinctly bilobed in young, lobes medianly fused in adult, myophores postero-dorsally directed ; adult lateral ridges strong, extending beyond hinge-line on to flanks of cardinal process and anteriorly diverging from hinge-line at about 15°, extending round inside of ears to lateral margins where they are externally crenulated ; adductor field raised, extending about one-third valve length and wider than long, divisible into trigonal and lobate anterior and posterior scars ; median septum about two-thirds valve length, high anteriorly ; brachial impressions from between anterior and posterior adductor scars, at about 60° to mid-line, lobate, ridges low ; trail tuberculate.

MEASUREMENTS (in mm.)

	length	width
Complete pedicle valve (BB.52832)	15·0	19·4
Complete brachial valve (BB.52833)	14·0	25·8
Pedicle valve interior } paired valves (BB.52834) .	—	23·0
Brachial valve interior } paired valves (BB.52835) .	14·0	21·0
Brachial valve (BB.52836)	5·7	8·3
Shell with broken pedicle valve (BB.52837)	14·5	19·1
Complete pedicle valve (BB.52841)	0·7	0·9
Complete pedicle valve (BB.52842)	1·8	2·1
Incomplete pedicle valve with bryozoan (BB.52843) .	—	2·5
Complete pedicle valve (BB.52844)	3·1	4·2

LOCALITY AND HORIZON. Subreefal limestones, Bunnahone, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. Of the three specimens of *Producta plicatilis* in the Sowerby Collection only one, B.M. (N.H.) B.60960, was figured by Sowerby (1824, pl. 459, fig. 2). This specimen was designated as lectotype by Thomas (1914 : 332) and the Fermanagh shells agree with it in all known respects, such as outline, profile, rugation and ribbing. The type specimen is about one-half the width of the other Sowerby specimens and these have about 28 rugae on each valve (cf. Table 9) but show no sign of ribbing. These two large specimens clearly differ from the type, possibly because of a differing environment, and may not be conspecific. There is a wide variation of size and development of the antero-ventral sulcus in specimens from different localities and it remains to be seen whether the ribbing is associated with other characteristics warranting specific distinction.

A comparison of the type specimen of *Plicatifera plicatilis* with the holotype of *P. pseudoplicatilis* Muir-Wood reveals that the two are conspecific and it is possible that Muir-Wood's comparison (1928 : 190) was based upon the two large Sowerby specimens. The only differences seen in these type specimens are that *P. pseudoplicatilis* has no sulcation and the brachial valve geniculation is slightly less than in *P. plicatilis*. However, these differences are covered by specific variation.

There is no true geniculation in the pedicle valve of *P. plicatilis* and its even convexity can be seen illustrated by Thomas (1914 : 331, text-fig. 13). Towards its anterior margin the brachial valve is commonly geniculated against the inner surface of the pedicle valve.

P. plicatilis is unusual in the depth of the body cavity, which in adult shells is over one-half of the length. The pedicle valve rugation stopped after the development of about 24 rugae, at the lowest, or most ventral part of the valve and immediately posterior to the " geniculation ". (It is commonly impossible to see the posterior three or four rugae because of abrasion to the ventral umbo.) At this stage the brachial valve did not form a trail against the pedicle valve, but continued to rotate dorsalwards around the hinge-line, so that the body cavity increased in depth until

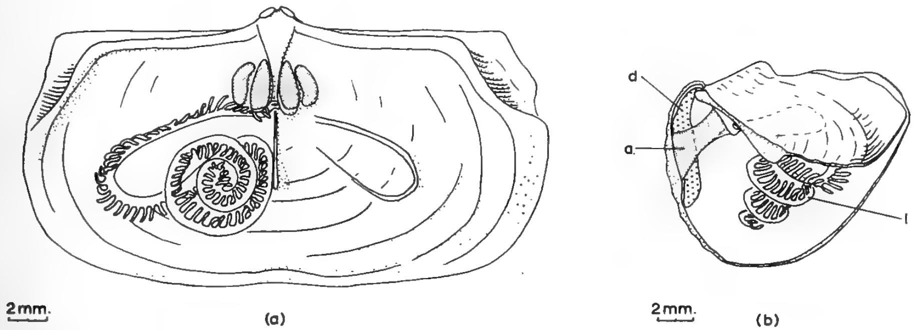

FIG. 8. Illustrations of (a) the brachial valve interior showing the adductor muscle scars, the inferred position of the stylized lophophore, and the postero-lateral crenulations across the inner margins of the ears ; (b) an internal lateral view of a stylized reconstruction of *Plicatifera plicatilis* (J. de C. Sowerby) ; *a*, adductor muscles ; *d*, diductor muscles ; *l*, stylized lophophore.

the dorsal visceral disc was at about 70° to the rugate portion of the pedicle valve. Thus the rugation only extends for about one-half the full length of the ventral visceral region, the rest being smooth with faint ribbing, and it is somewhat misleading to describe all the smooth region as a trail. As the dorso-anterior curvature of the pedicle valve formed the arc to the rotating brachial valve, growth in the latter was confined to extension of the developing trail, and was probably slower than that of the pedicle valve.

P. plicatilis was furnished with a pedicle sheath in its earliest stages of growth (Pl. 7, figs. 1, 4) and at a length of about 2 mm. the ventral valve had three pairs of clasping spines which arched over the beak. The first pair was developed on the brephic valve, lateral to the shallow groove extending antero-ventrally from the pedicle sheath, and formed a circle of about 0·2 mm. in diameter. Rarely, thin fragments of bryozoans are preserved held by these spines (Pl. 7, fig. 3). The second pair developed close to the hinge-line, about 1·0 mm. apart, and curved to form a ring, commonly in contact with the posterior circumference of the first ring (Pl. 7, fig. 12), unless deflected by some foreign object. The third pair, again close to the hinge-line, developed about 1·8 mm. apart, at a valve length of about 1·4 mm. and curved postero-ventrally, commonly to within 0·5 mm. of the valve surface, but less regularly than the previous spines because of deflection against solid objects, usually the object held by the preceding spines and used as anchor by the young shell (Pl. 7, figs. 7, 8). By this stage a pair of normal antero-ventrally directed sub-erect spines, and a single median spine, had developed. All subsequent spines were of this type and developed more or less symmetrically in pairs from the crests of the rugae. However, both spines of a pair were not always situated on the same ruga, and the spacing became more widely separated anteriorly. On the flanks of the adult smooth region two rows of three or four laterally directed spines developed, together with one or two pairs of anteriorly directed spines.

The ventral adductor scars are evident in valves about 6 mm. long but are not easily distinguishable from the diductor scars. By adulthood, when the non-rugate anterior region had developed, the adductor scars were distinctly raised. The dorsal adductor scars became defined at an earlier stage and can be seen in valves of only 2 mm. long. The raised, elongately oval to trigonal, anterior scars developed first. The posterior scars only became visible in adulthood, at first as tuberculate ridges flanking the anterior scars, but later as raised pear-shaped or trigonal areas a little shorter than, and lateral to the anterior scars. Both scars are rather variable in detail, but the complete field is commonly a little over three-quarters as long as wide and about one-third as long as the visceral disc.

The median septum developed between the adductor scars from a valve length of about 6 mm. In adult shells, 11 to 12 mm. long, the septum is two-thirds the valve length, but is completely buried by secondary shell for most of its length between the adductor scars. It reached its greatest height, of about 1 mm., anteriorly, between the brachial impressions, and is marginally thickened. Posteriorly a wide ridge of secondary shell connects the adductor platform to the base of the cardinal process and to the median ends of the lateral ridges (Pl. 6, fig. 15).

The juvenile cardinal process is distinctly bilobed, but fused ventro-medianly over a deep alveolus which penetrates almost to the dorsal beak and represents the inside of the protegulal node (Pl. 6, fig. 12). Indeed, the internal distinction of the lobes is so complete that it seems clear that the cardinal process grew from a rudiment at the posterior end of the protegulal node as two elevated ridges, supported by the rudiments of the lateral ridges, which were enlarged antero-ventrally to cover the cavity postero-ventrally. Posteriorly, along either side of the nodal cavity, the lobes were fused and formed an arch together with the median ends of the lateral ridges. From this arch the incised myophore lobes extended ventrally, separated by a deep sulcus (Pl. 6, fig. 11). Continued shell deposition at the edges of the myophores, around the muscle bases, caused them to become both increasingly deeply incised and the progressive fusion of the two median muscle boundaries with one another. This fusion occurred at variable stages of growth, and the cardinal process commonly remained distinctly bilobed until adulthood, and only then were the inner, or ventral, margins of the lobes united medianly. Also at this stage, the deposition of secondary shell, anterior to the cardinal process, filled the alveolus, the remnant of the protegulal body cavity.

The lateral ridges began development in valves 4 to 5 mm. long, and diverged from the hinge-line at 15°. During growth they became increasingly prominent, extending over one-half the distance to the cardinal extremities by the time the rugate region of the pedicle valve was developed. Subsequently, curvature of the pedicle valve increased and the externally crenulated ridges across the insides of the ears developed. When the visceral disc had attained a width of 20 mm. the ridges had fused with these ear ridges (" ear baffles " of Muir-Wood) to form a continuous ridge from the cardinal process to the widest part of the visceral disc on the lateral margins. As the brachial valve rotated dorsally during growth these ridges became increasingly prominent and maintained a sealed posterior margin, and articulatory surfaces. The ridges became deeply concave posteriorly for the reception of the angular lateral ridges which had developed simultaneously within the pedicle valve (Pl. 7, fig. 18). The crenulations on their outer surfaces, at the postero-lateral margins, became marked and fitted those similarly placed on the flanks of the pedicle valve interior. In the pedicle valve, the traces of these crenulations indicate the brachial valve rotation during growth, not the amount of possible movement of the brachial valve in life.

TABLE 7

$\overline{\mathrm{L}}$ mm. (var.) = 8·66 (17·006)	$\overline{\mathrm{Ad.L}}$ mm. (var.) = 2·51 (1·867)
$\overline{\mathrm{W}}$ mm. (var.) = 15·48 (75·196)	$\overline{\mathrm{Ad.W}}$ mm. (var.) = 3·14 (2·974)
r = 0·983	r = 0·997
a (var.) = 2·103 (0·0250)	a (var.) = 1·262 (0·00166)

TABLE 7. Statistics of length (L), maximum width (W), length of adductor scars (Ad.L), and width of adductor scars (Ad.W) of 8 brachial valves of *Plicatifera plicatilis* (J. de C. Sowerby).

TABLE 8

$$\overline{L} \text{ mm. (var.)} = 5{\cdot}90\ (16{\cdot}220)$$
$$\overline{W} \text{ (var.)} = 9{\cdot}04\ (51{\cdot}363)$$
$$r = 0{\cdot}986$$
$$a \text{ (var.)} = 1{\cdot}779\ (0{\cdot}01267)$$

TABLE 8. Statistics of length (L) and width (W) of 9 pedicle valves of *Plicatifera plicatilis* (J. de C. Sowerby).

TABLE 9

Number of rugae	20	21	22	23	24	25	26
Number of specimens	1	0	2	6	4	3	2

TABLE 9. The number of rugae counted on 18 pedicle valves, in which all the rugae had developed, of *Plicatifera plicatilis* (J. de C. Sowerby).

Subfamily **PRODUCTININAE** Muir-Wood & Cooper 1960

Genus ***PRODUCTINA*** Sutton 1938

1928 *Thomasia* Fredericks : 790.
1931 *Thomasina* Paeckelmann : 181.
1938 *Productina* Sutton : 551.
1942 *Thomasella* Paul : 191.
1951 *Argentiproductus* Cooper & Muir-Wood : 195.
1960 *Argentiproductus* Cooper & Muir-Wood ; Muir-Wood & Cooper : 182.

EMENDED DIAGNOSIS. Outline subsemicircular to suboval, hinge-line straight, commonly widest part of shell, umbo prominent ; profile strongly concavo-convex with narrow body cavity ; costae commonly prominent on pedicle valve, rarely branching dichotomously, widening and flattening towards anterior margin and bearing suberect spines posteriorly ; strong spine rows across umbonal slopes towards postero-lateral margins, and more or less symmetrically placed spines postero-medianly ; concentric lamellae, prominent on brachial valve which is obscurely ribbed ; ventral adductor scars elongately trigonal, slightly raised ; diductor scars indistinct, flabellate ; lateral ridges diverging from umbo across anterior margins of ears ; cardinal process sessile but strongly bilobed, each lobe dorso-posteriorly incised ; lateral ridges diverging from flanks of cardinal process at low angle from hinge-line ; adductor scars trigonal to elongately oval, slightly

raised; median septum ill-defined, not fused to base of cardinal process, about three-fifths valve length.

TYPE SPECIES. *Productus sampsoni* Weller 1909, by original designation of Sutton (1938 : 551).

DISCUSSION. The present material was collected from beds of approximately the same stratigraphic position, and 12 miles north-west of the locality in Co. Fermanagh from which Phillips collected *Producta margaritacea* the type species of *Argentiproductus* Cooper & Muir-Wood 1951. Despite obvious external similarities with *Argentiproductus*, as conceived by Muir-Wood & Cooper, (1960 : 182), the dorsal interiors actually agree more closely with those of *Productina* Sutton from which they differ only in their greater size. Moreover Sutton (1938 : 551) states that *P. margaritacea* may be congeneric with his genus. Weller's original description of the type species, *Productus sampsoni*, gives no information about internal morphology, but there is no doubt that all the specimens referred to by him were no more than 13 mm. long. Their outline is perhaps more rounded than that of *P. margaritacea*, but the cardinal extremities of all specimens illustrated by Weller and by Muir-Wood & Cooper appear to be broken, so that they may, in fact, be more transverse than is stated. The two genera, *Productina* and *Argentiproductus*, are distinguished by Muir-Wood & Cooper (1960 : 182) on characteristics that vary with size, such as the width of ribbing, the convexity of the shell, etc. together with more important differences between the dorsal interiors. The dorsal interior of *Argentiproductus* figured by them (pl. 123, figs. 17, 17*a*), however, is of a brachial valve from Visé, Belgium and is quite unlike the interiors of brachial valves in the Fermanagh fauna. On the other hand, the illustrated dorsal interior of *Productina* (*P. sampsoni*, pl. 123, figs. 7, 9) is closely comparable to interiors of immature Fermanagh valves (Pl. 8, fig. 9). It seems, therefore, that the dorsal interior attributed to *Argentiproductus* does not belong to the type species of that genus, and the American and British species do not warrant separation at generic level.

Productina margaritacea (Phillips)

(Pl. 8, figs. 1–19; Pl. 15, figs. 1–8)

1836 *Producta margaritacea* Phillips : 215, pl. 8, fig. 8.
1861 *Productus margaritaceus* Phillips; Davidson : 159, pl. 44, figs. 5–8.
1951 *Argentiproductus margaritaceus* (Phillips) Cooper & Muir-Wood : 195.
1960 *Argentiproductus margaritaceus* (Phillips); Muir-Wood & Cooper : 182, pl. 123, figs. 11–16, *non* fig. 17.

EMENDED DIAGNOSIS. Outline subsemicircular with widest point at or near straight hinge-line, length about three-fifths width, umbo arched, rounded and extending well beyond hing-line, lateral slopes steep, ears narrowly tringular; adult profile strongly concavo-convex, depth about one-half length; ribs more prominent on pedicle valve, low flattened anteriorly with narrow interspaces, about 6 per 2·5 mm., 4 mm. antero-medianly from ventral umbo; concentric ornament

lamellose, prominent on brachial valve, variable on pedicle valve; young with pedicle-sheath from ventral beak; spines posteriorly confined; prominent rows of about five spines along each umbonal slope and anterior to ears, commonly one or two median spines, others sparsely paired within first 8 mm. of length, ventral adductor scars slightly raised, lanceolate to elongately trigonal, flanked by rounded, elongately trigonal anteriorly spreading diductor scars; articulatory ridges diverge from umbo at about 20° to hinge-line and die out laterally across anterior margin of ears; prominent lateral spines retain internal connections; cardinal process sessile but prominently bilobed, each myophore incised forming V-shaped, quadrifid postero-dorsally directed surface; supporting ridges diverge from hinge-line at about 30° for about one-half hinge width; adductor scars rounded trigonal, about as long as wide and extend one-third valve length, slightly raised, especially in young; median septum ill-defined, arising between adductor scars and extending over one-half adult length; median and anterior surfaces of valves tuberculate, shell substance pseudopunctate.

MEASUREMENTS (in mm.):

	length	width
Incomplete shell (BB.52904)	17·3	—
Incomplete shell (BB.52905)	14·3	20·2
Incomplete pedicle valve (BB.52906)	*c.* 8·0	*c.* 12·0
Incomplete pedicle valve (BB.52907)	*c.* 7·3	*c.* 10·0
Incomplete pedicle valve (BB.52908)	—	*c.* 9·0
Complete brachial valve (BB.52909)	13·0	22·8
Complete brachial valve (BB.52910)	3·0	5·2
Incomplete brachial valve (BB.52911)	1·8	*c.* 2·8
Complete pedicle valve (BB.52912)	4·1	6·0
Incomplete pedicle valve (BB.52913)	2·4	*c.* 3·8
Incomplete pedicle valve (BB.52914)	3·4	3·8
Incomplete pedicle valve (BB.52915)	1·9	—

LOCALITIES AND HORIZON. Subreefal argillaceous limestone at Bunnahone and Carrick Loughs, about 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. Disarticulated valves and shells ranging from under 2 mm. to about 20 mm. in length provide ample material for ontogenetic studies. During larval settlement onto a suitable substratum, which was probably firm or solid, the protegulal node developed as a bilobed structure about 0·3 mm. in length, from the posterior end of which was secreted a narrow pedicle sheath (Pl. 8, fig. 18). From the postero-ventral surface of this shell rudiment was developed the brephic valve, commonly about 1·0 mm. long and 0·75 mm. wide, with a postero-ventrally directed longitudinal groove across its length, inherited from the bilobate protegulum. One or two pairs of spines within 0·5 mm. of the pedicle sheath, and 0·2 to 0·3 mm. apart, formed complete encircling rings over the groove (Pl. 15, fig. 6). These spines are

thought to have grown in this way as a genetically controlled feature rather than in response to the form of the substratum, but in some larvae they might have encircled erect cylinders like spines in a productoid colony when chance settlement afforded such a substratum. In any event, the pedicle rudiment was soon lost because its internal opening became sealed at about this stage of growth, as can be seen in one valve, 2 mm. long. This closure is unlikely to have been due to silicification because openings to the nearby encircling spines are marked by distinct depressions.

The external groove is represented internally by a ridge which was continued during valve growth as low adductor platforms, but which was distinguishable as such only in valves about 2 mm. long. At this stage the diductor scars are elongately trigonal and rounded, extending anteriorly of the adductor scars along the insides of the umbonal slopes (Pl. 8, fig. 16).

The onset of neanic growth stages is shown in valves between 0·8 and 1 mm. long by a prominent growth-line and by the first pair of laterally directed spines. The radial ornamentation was initiated at this stage, but is seldom visible until the valves attained a length of 1·5 to 2 mm. Commonly at a length of just over 1 mm., a second pair of spines arose on either side of the mid-line, near the first median spine, which is anteriorly directed, and just before the formation of the first pair of longer spines on the umbonal slopes. These are the first of the two rows of spines flanking the umbo and front of the ears. Subsequent growth continued with the periodic development of symmetrically placed paired spines, and occasional median spines, in such a way that the increase of valve area led to a reduction of spine density towards the anterior margin. With the exception of the row of strong flanking spines (and a single median spine which was commonly developed 8 mm. from the umbo), the spines ceased to grow in valves more than 4 mm. long so that the total number of spines, excluding the brephic ones, is about eighteen. Strictly speaking the first formed pair of laterally directed spines on the neanic shell should probably be included as members of the rows of flanking spines. This has not been done on the measured specimens as it was frequently impossible to locate their position accurately, which is about 0·4 mm. from the beak (Table 12). All the spines arose as a thickening and anterior prolongation of a rib crest and are at an angle of less than 60° to the valve surface.

Internally, the laterally directed ridges which demarcate the anterior extremities of the ears, grew to about three-fifths of the valve width. In so doing they sealed the internal openings of the more medianly placed flanking spines so that only the younger one or two pairs retained their internal connections, and hence their powers of growth.

Brachial valves are furnished with a small oval protegulal node, about 0·3 mm. long, and a rounded, smooth brephic valve about 0·8 mm. long. Beyond this length low lamellose concentric ridges were formed across which the indistinct ribs can be traced. There are no spines. In valves of 1·8 mm long, the adductor scars are prominent as slightly raised oval markings reaching nearly one-half the valve length (Pl. 15, fig. 8). The lateral ridges diverge from the hinge-line at about 20° and extend for one-half of its width, i.e. about 0·6 mm. on either side of the distinctly bilobed

cardinal process. The posterior growth of the cardinal process, together with that of the median ends of the lateral ridges, extended the latter beyond the hinge-line when the valve was about 3 mm. long. By adulthood the ridges extended about half way up the flanks of the cardinal process and are externally visible for approximately one-fifth of the hinge width. These ridges not only supported the cardinal process, but more importantly aided the articulation of the valves and are essentially the same structures as the socket ridges of the Strophalosiidae. They form wide flat areas, lateral to the cardinal process, against which the more medianly placed parts of the lateral ridges of the pedicle valve articulated (Pl. 8, figs. 8–9).

The median septum is never strongly developed and arose at a valve length of about 3·0 mm. as a low ridge about 1 mm. long and extending for two-thirds of the valve length. It grew from a point between the anterior ends of the adductor scars and during growth extended posteriorly between the scars and slightly anteriorly to a distance of just over one-half the valve length. The septum never seems to have fused to the base of the cardinal process. While remaining distinct during growth, the adductor scars became less raised because of the surrounding deposition of secondary shell.

The strong curvature of the pedicle umbo commonly protected it from abrasion so that even adult shells, about 18 mm. long (measured as a chord to their curvature), may retain the stumps of the brephic spines and pedicle sheath.

The radial ornamentation is more prominent on pedicle valves than brachial valves, where the lamellose ornamentation is more pronounced. An increase in the number of the ribs is by rare dichotomy, largely confined to the posterior spinose region. All ribs increase in width towards the anterior margin by four or five times their original width, and become increasingly flat topped. The interspaces always remain narrower than the ribs. Dichotomy commonly occurred posterior to one of the lamellae. However, the dichotomy commonly did not continue beyond the lamella, and here the rib may once again be single. In this way a rib may have formed several incipient branchings, by the division of the fold at the anterior margin of the mantle, which were suppressed by the retraction of the mantle which formed the lamellae. Commonly the renewed forward growth of the mantle continued in the prebranched condition so that a single rib formed at the valve surface. Thus, the number of ribs at the anterior margin of a shell is usually less than would be expected from the number of incipient branchings that occurred along the costae.

TABLE 10

$\bar{L}$ mm. (var.) = 7·45 (25·075)	$\bar{L}$ mm. (var.) = 7·45 (25·075)
$\bar{W}$ mm. (var.) = 11·03 (66·876)	$\bar{Th}$ mm. (var.) = 3·08 (5·589)
r = 0·991	r = 0·911
a (var.) = 1·633 (0·00185)	a (var.) = 0·472 (0·00146)

TABLE 10. Statistics of length (L), width (W) and thickness (Th) of 28 pedicle valves of *Productina margaritacea* (Phillips).

TABLE 11

Ribs	4	5	6	7	8	9
At 4 mm.	0	1	8	5	6	1
At 6 mm.	3	5	5	1	0	0

TABLE 11. Ribs counted per 2·5 mm. width at 4 mm. and 6 mm. antero-medianly from the ventral umbo of *Productina margaritacea* (Phillips).

TABLE 12

Mid-line to	1st spine	2nd spine	3rd spine	4th spine	5th spine
Mean (mm.)	0·90	1·72	3·40	8·30	12·73
(var.)	0·010	0·0984	0·6711	6·5933	11·53
N	25	27	21	5	3

TABLE 12. Statistics of distances from the mid-line to the first, second, third, fourth and fifth spines on the line of prominent spines flanking the umbonal slopes to the postero-lateral margins of *Productina margaritacea* (Phillips). (A neanic pair of spines at about 0·4 mm. from the mid-line should perhaps be included in this series.)

TABLE 13

$$\bar{L}\text{ mm. (var.)} = 3{\cdot}67\ (6{\cdot}183)$$
$$\bar{W}\text{ mm. (var.)} = 6{\cdot}24\ (20{\cdot}820)$$
$$r = 0{\cdot}995$$
$$a\text{ (var.)} = 1{\cdot}835\ (0{\cdot}0020)$$

$$\bar{L}\text{ mm. (var).} = 3{\cdot}67\ (6{\cdot}183)$$
$$\overline{AdL}\text{ mm. (var.)} = 1{\cdot}22\ (0{\cdot}427)$$
$$r = 0{\cdot}950$$
$$a\text{ (var.)} = 0{\cdot}276\ (0{\cdot}00044)$$

$$\overline{AdL}\text{ mm. (var.)} = 1{\cdot}22\ (0{\cdot}472)$$
$$\overline{AdW}\text{ mm. (var.)} = 1{\cdot}41\ (0{\cdot}365)$$
$$r = 0{\cdot}983$$
$$a\text{ (var.)} = 0{\cdot}897\ (0{\cdot}00155)$$

TABLE 13. Statistics of length (L), maximum width (W), length of the adductor scars from the hinge-line (AdL) and their total width (AdW) in 19 brachial valves of *Productina margaritacea* (Phillips).

TABLE 14

$$\bar{L}\text{ mm. (var.)} = 5{\cdot}53\ (16{\cdot}411)$$
$$\overline{MsL}\text{ mm. (var.)} = 2{\cdot}90\ (4{\cdot}139)$$
$$r = 0{\cdot}969$$
$$a\text{ (var.)} = 0{\cdot}502\ (0{\cdot}00153)$$

TABLE 14. Statistics of length (L) and length of the median septum (MsL) from the hinge-line of 12 brachial valves of *Productina margaritacea* (Phillips).

Family **OVERTONIIDAE** Muir-Wood & Cooper 1960

Subfamily **OVERTONIINAE** Muir-Wood & Cooper 1960

Genus ***OVERTONIA*** Thomas 1914

TYPE SPECIES. *Producta fimbriata* J. de C. Sowerby 1824, by original designation of Thomas (1914 : 259).

Overtonia fimbriata (J. de C. Sowerby)

(Pl. 9, figs. 1–13 ; Pl. 10, figs. 1–7 ; Text-fig. 9)

1824 *Producta fimbriata* J. de C. Sowerby : 85, pl. 549, fig. 1.
1861 *Productus fimbriatus* J. de C. Sowerby ; Davidson : 171, pl. 33, figs. 12–15 *non* pl. 44, fig. 15.
1914 *Overtonia fimbriata* (J. de C. Sowerby) Thomas : 259, 335, pl. 20, figs. 12–17.
1960 *Overtonia fimbriata* (J. de C. Sowerby) ; Muir-Wood & Cooper : 183, pl. 46, figs. 10–20.

EMENDED DIAGNOSIS. Outline subrounded, length of adult shell almost equal to maximum width, commonly at mid-length, umbo rounded extending well beyond straight hinge-line which commonly forms maximum width of young shells ; ears small triangular ; profile subsemicircular, plano-convex to slightly concavo-convex, a little over one-half as deep as long, body cavity deep, short dorsally directed trail ; concentric rugae rounded and prominant posteriorly, becoming wider, flatter and increasingly lamellose anteriorly ; about three high-angled, antero-ventrally directed spines per 5 mm. at 5 mm. antero-medianly of ventral umbo ; from about sixth ruga, and anterior to each spine, lamellae tightly folded into prostrate spine-like extensions projecting between spines of anterior ruga, so forming longitudinally disposed short ridges between spine rows ; growth-lines well developed between rugae ; brachial valve almost flat across disc, geniculated against pedicle valve, ornamented by closely spaced concentric lamellae and low rugae bearing more closely spaced dorsally directed spines ; rugae forming acute angle with hinge-line towards cardinal extremities ; ventral interior poorly developed and preserved, ridges diverging narrowly from beak and extending at low angle from hinge-line towards inner margins of ears ; muscle field indistinct, adductor scars elongately trigonal with more rounded, spreading diductor scars ; anteriorly tuberculate and with spine openings ; two lobes of cardinal process more or less fused dorsally but separated by groove ventro-posteriorly, myophores deeply incised to tube-like ; lateral ridges diverging from base of cardinal process at 20° to hinge-line and extending round inside of ears to form low visceral ridge around disc ; adductor platform prominently raised, postero-ventrally facing, divisible into elongately trigonal anterior scars and small trigonal posterior scars, whole muscle field about twice as wide as long ; median septum short, prominent anteriorly as bulbous prolongation, about one-third valve length ; brachial impressions from anterior flanks of adductor platform, antero-laterally to anteriorly directed, lobate ; strongly tuberculate anteriorly ; shell substance pseudopunctate.

MEASUREMENTS (in mm.)

	length	width
Complete shell (BB.52845)	16·5	17·0
Complete pedicle valve (BB.52846)	14·3	15·8
Complete brachial valve (BB.52847)	11·9	15·0
Complete brachial valve (BB.52849)	8·2	9·0
Complete shell (BB.52850)	9·6	10·5
Complete shell (BB.52851)	5·6	6·2
Incomplete brachial valve (BB.52848)	10·5	14·5

LOCALITY AND HORIZON. Subreefal limestones, Bunnahone, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. The type specimen of *O. fimbriata* (J. de C. Sowerby) is apparently lost (Thomas 1914 : 339) and the two specimens in the Sowerby Collection (B.M.N.H., No. 60978–79) named *Producta fimbriata* are thought to be misidentified. Neither of these specimens match Sowerby's (1824 : 85) description or figure and one (B.60978) is probably an echinoconchid, while the other (B.60979) is probably *Overtonia* but not *O. fimbriata*. Both are poorly preserved and not localized. Thomas (1914 : 259) based his generic description of *Overtonia* upon several specimens, making special reference to material in the Davidson Collection (B.M.N.H. Nos. B.5762, B.13854), but he did not designate a neotype. In his specific description of *O. fimbriata* Thomas said that the Davidson specimens (B.13854) were typical and should it become necessary to stabilize nomenclature by the designation of a neotype, it is from these specimens that it should be chosen.

Thomas (1914) noted that the greatest width in young shells may temporarily be at the hinge-line and that the length of the pedicle valve is slightly greater than its maximum width. In the present sample the width is greater than the length indicating the variation which can occur between these attributes within the species as a whole (Table 16). There is a high correlation between length and depth and these dimensions display an allometric relationship resulting from the high degree of curvature of the pedicle valves, which in adult specimens is more than 360°.

A young pedicle valve, about 9·0 mm. long shows a shallow umbonal groove, flanked by a pair of spine bases. There are signs of a pedicle sheath on this specimen, as also on a few other pedicle valves.

Ornamentation is distinctive. On pedicle valves the rugae became increasingly spaced during growth and the spines, which arose from the rugae, more widely separated, so that few spines were added beyond a shell length of about 5 mm. Within a width of 5 mm., 3 and 4 spines were counted in 9 and 3 pedicle valves respectively at a distance of 5 mm. antero-medianly of the ventral umbo. The spines extended anteriorly at about 60° to the valve surface, but soon increased their curvature to reduce this angle. They are radially arranged, but miss every second ruga, so that they form two diagonal sets at 35° to 40° from one another (Pl. 9, fig. 4). Commonly the sixth and subsequent rugae became anteriorly lamellose and developed tight radially arranged folds anterior to each spine. These folds formed spine-like ridges that extended anteriorly from the spines of one ruga to a point between the

spines on the next anterior ruga (Pl. 9, figs. 2, 4). Thomas (1914 : 335) and Muir-Wood & Cooper (1960 : 184) refer to "spine bases" or "spine ridges" without mentioning the antero-dorsally directed, lamellose spine-like projections with which they are associated. The ridges are not the spine bases for the normal erect spines. However, Thomas was correct in stating that the "spine bases" occasionally extend across "the depresssions between the rugae" but are never sufficiently continuous to form true costation". It is, in fact, clear that a costation could not have been formed by these ridges because of their en-echelon arrangement, and that Muir-Wood & Cooper (1960 : 184) erred in saying that these spine ridges extend "across bands or from one band to the next, thus simulating costae".

The brachial valves are similarly ornamented, except that the concentric lamellae and spine rows are more closely spaced. This is because their total number is the same as on the corresponding pedicle valve, while the surface length of the valve is considerably less (Text-fig. 6). There are 5 or 6 spines in 5 mm. width, 5 mm. from the dorsal umbo. The lamellae are not folded into spine-like ridges, as on the pedicle valve.

Internally the brachial valve shows a number of unusual features. The two lobes of the cardinal process are medianly fused for most of their length so that the myophores are narrowly V-shaped but very deeply incised. The area of attachment of the diductor muscle bases must, therefore have been strongly arcuate so that

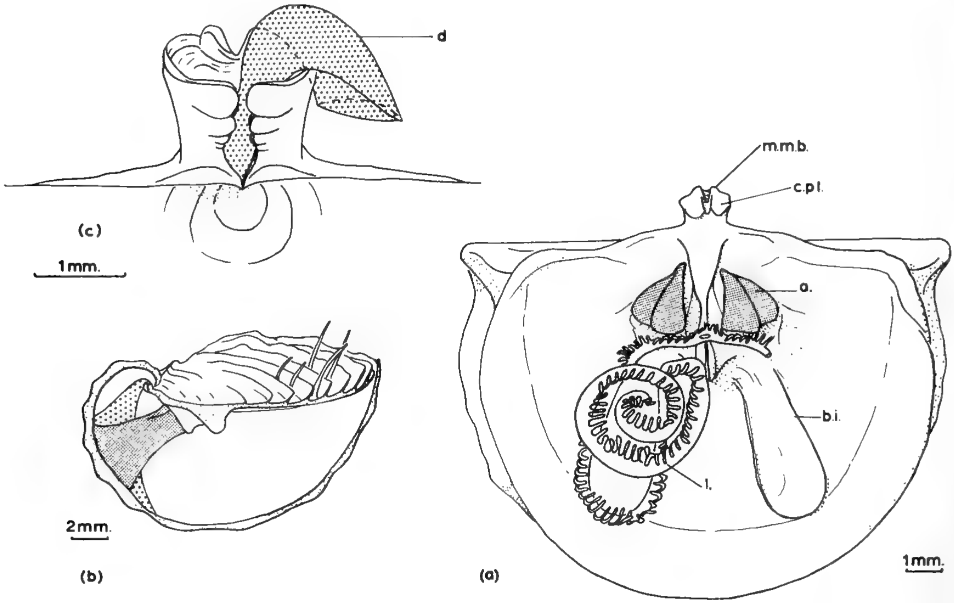

FIG. 9. Illustrations of (a) brachial valve interior; (b) lateral view of shell interior and (c) external view of cardinal process, with the diductor muscle attached to one lobe, of *Overtonia fimbriata* (J. de C. Sowerby) *a*, divided adductor scars; *b.i*, brachial impressions; *c.p.l.*, cardinal process lobe; *d*, diductor muscle extending from cardinal process towards the floor of the pedicle valve; *l*, stylized lophophore; *m.m.b*, median muscle boundary.

shell deposition formed open-sided tubes, the sides opening dorso-medianly down the centre of the dorsal surface of the cardinal process along a common groove (Pl. 9, figs. 6–8). The diductor muscles extended from the posterior ends of these tubes and curved ventrally to the floor of the pedicle valve (Text-fig. 9, *c*). Internally the two lobes are more widely separated and, where they fused proximally, there are two small ventrally directed nodes.

The adult dorsal adductor field faces postero-ventrally at about 60° to the commissural plane, so that its anterior margins are built up by a thick deposit of secondary shell (Pl. 9, figs. 8, 9). This high degree of tilting was presumably in response to the unusually deep body cavity, which was accentuated during growth by the dorsal rotation of the brachial valve about the hinge-line. The tilt of the adductor platform maintained the muscle scars more or less parallel to the ventral adductor scars and allowed these muscles to retain a higher degree of efficiency than would otherwise have been possible (Text-fig. 9, *b*).

Between, and anterior to, the adductor platform, and divided by the median septum, is a deep triangular to rhomboidal area which has been likened to that found in a similar position in *Leptagonia analoga* (Davidson 1861 : 172). It seems likely that these depressions on either side of the median septum housed the trunks of the *vascula media*. The median septum itself is much enlarged anteriorly, while posteriorly it is covered by shell substance between the posterior margins of the adductor platforms. In a young valve 8 mm. long, the adductor platforms are free of the valve floor anteriorly, and below their arching anterior margins can be distinguished antero-laterally directed probuberances which project immediately above, and in line with, the outer margins of the faint brachial impressions (Pl. 10, fig. 3). These protuberances may have supported the median, oral segment of the lophophore, before the full growth of the cardinalia, by which time they had become covered by shell supporting the adductor platforms. In the adult shell, the lophophore was probably attached to the anterior edge of these platforms, the mouth being between their anterior margins and ventral to the median septum. The lophophore continued around the brachial markings to curve medianly and anteriorly onto the prominent anterior end of the median septum. From this point two spires probably hung into the deep pedicle valve (Text-fig. 9). This arrangement necessitates the final free spires to have been coiled in the opposite sense to those suggested for *Productus* s.s. by Williams (1956, text-fig. 5 (6)).

TABLE 15

No. of rugae	6	7	8	9	10	11	12	13	14
No. of specimens	3	2	1	2	1	5	0	0	1
Approx. length of of specimens	6	8·5	11·5	12·0	13·0	14·0	—	—	17·0

TABLE 15. The number of rugae counted on 15 pedicle valves of *Overtonia fimbriata* (J. de C. Sowerby), together with the approximate length of the valves at each additional ruga.

TABLE 16

$\overline{L}$ mm. (var.) = 11·38 (12·349)
$\overline{W}$ mm. (var.) = 12·63 (15·005)
r = 0·986
a (var.) = 1·102 (0·00262)

$\overline{W}$ mm. (var.) = 12·63 (15·005)
$\overline{HiW}$ mm. (var.) = 11·33 (11·088)
r = 0·949
a (var.) = 0·860 (0·00563)

$\overline{L}$ mm. (var.) = 11·38 (12·349)
$\overline{Th}$ mm. (var.) = 6·04 (5·384)
r = 0·992
$\text{Log}_e\ \overline{L}$ (var. $\log_e L$) = 2·388 (0·908)
$\text{Log}_e\ \overline{Th}$ (var. $\log_e L$) = 1·729 (0·1381)
r_e = 0·997
α (var.) = 1·229 (0·00070)

TABLE 16. Statistics of length (L), maximum width (W), width of hinge-line (HiW) and thickness (Th) of 15 pedicle valves of *Overtonia fimbriata* (J. de C. Sowerby).

TABLE 17

$\overline{L}$ mm. (var.) = 10·63 (3·272)
$\overline{W}$ mm. (var.) = 13·38 (5·338)
r = 0·945
a (var.) = 1·277 (0·0436)

$\overline{AdL}$ mm. (var.) = 1·82 (0·234)
$\overline{AdW}$ mm. (var.) = 3·47 (0·842)
r = 0·955
a (var.) = 0·600 (0·00793)

$\overline{L}$ mm. (var.) = 10·63 (3·272)
$\overline{AdL}$ mm. (var.) = 1·82 (0·234)
r = 0·975
a (var.) = 0·276 (0·00088)

$\overline{SpL}$ mm. (var.) = 3·63 (0·605)

TABLE 17. Statistics of length (L), width (W), length of adductor scars (AdL), width of adductor field (AdW) and length of the median septum (SpL) from the hinge-line of 6 brachial valves of *Overtonia fimbriata* (J. de C. Sowerby).

Genus *AVONIA* Thomas

1914 *Avonia* Thomas : 259.
1928 *Avonia* Thomas ; Muir-Wood : 36.
1960 *Avonia* Thomas ; Muir-Wood & Cooper : 185.

TYPE SPECIES. *Productus youngianus* Davidson 1860, by original designation of Thomas (1914 : 259).

DISCUSSION. The genus was briefly described by Thomas and emended by Muir-Wood, but not until 1960 was a full description of the genus available. One specimen figured as *Avonia youngiana* Muir-Wood & Cooper (1960, pl. 47, figs. 22–24) is not conspecific and should be referred to *Institifera tessellata* (de Koninck). The specimen, (BB.13593), has a deeper body cavity than *A. youngiana* ; a flatter brachial valve ; less elongate outline and more prominent and wider ribs. It agrees in all known respects with the specimen figured by Davidson (1861, pl. 33, fig. 25).

Interior features of the type species are poorly known and some of the species assigned to the genus by Muir-Wood & Cooper are doubtful. However, the original diagnosis of the genus stressed the characteristic external ornamentation which is spinose in the early stages but developed ribbing in late growth stages, towards the anterior margins. Davidson records that his species was abundant at Corrieburn, Stirlingshire (1860 : 181) and his figured specimen (1861, pl. 33, fig. 21) came from there. A single brachial valve interior, assigned to the species, is in the Davidson Collections (B.45681) and also came from Corrieburn. This brachial valve is closely comparable to specimens collected from Co. Fermanagh and attributed to *Avonia*.

The Irish shells display the distinctive ornamentation mentioned above, but differ from *A. youngiana* in attaining a larger size and in having a more rounded to transversely rectangular outline. Concentric lamellae are prominent and the specimens are probably conspecific with *Productus aculeatus* Sowerby.

A holotype does not appear to have been chosen for *A. youngiana*. A specimen from Corrieburn, in the Davidson Collection (B.45680), may well be the one upon which Davidson based his figures, both in 1860 (pl. 2, fig. 26) and in 1861 (pl. 33, fig. 21). It was figured by Muir-Wood (1928, pl. 12, figs. 9, 10) and is a complete shell showing the external ornamentation tolerably well. It should therefore, he considered as lectotype of *Avonia youngiana*.

There has always been some doubt regarding the validity of *A. youngiana* and *P. aculeatus*. Davidson discussed these species at some length (1863 : 233, 1880 : 311) but while retaining some doubts, he separated the two as distinct species. Thomas (1914) made *P. youngianus* the type species of *Avonia* and here *P. aculeatus* is included within that genus and designated as the type species of the new subgenus *Quasiavonia*. This is done only with the present system of Productoid classification in mind. It may prove more expedient in the future to consider many taxonomic groups as being more closely related than is now the practice. If so a greater use may be made of the subspecific status for forms that apparently differ only because of their environment. Such subspecies should converge morphologically in intermediate geographical or environmental regions.

Martin's specimen of *P. aculeatus* (BMNH. No. B.60992), used by Sowerby in 1814 for his description of the species, was chosen as lectotype by Muir-Wood (1951 : 101). Although this specimen is slightly abraded it is distinguishable from *A. youngiana.* by its more rounded outline, less well developed ribs and flatter brachial valve. However, the frequency of spines is more similar than was suggested by Davidson (1863), as can be seen from specimens of *A. Quasiavonia aculeata* from Settle, Yorkshire (B.5748), Dalry, Ayreshire (B.13940), and from the Fermanagh fauna (Pl. 11, figs. 3, 4).

Subgenus *QUASIAVONIA* nov.

Diagnosis. Outline rounded quadrate to subcircular, prominent rounded ventral umbo, maximum width slightly greater than length, commonly at hinge-line; profile concavo-convex, about one-half as deep as wide, and with moderately deep body cavity; concentric lamellae more prominent on pedicle valve; spines suberect

to recumbent, concentrically arranged and more or less radially aligned anteriorly, no true ribbing; ventral adductor field indistinct, scars slightly raised, elongate; dorsal adductor scars raised, elongately trigonal; median septum low, extending beyond adductor scars.

TYPE SPECIES. *Productus aculeatus* Sowerby 1814.

DISCUSSION. *Avonia* (*Quasiavonia*) *aculeata* is here considered as a distinct species group, having strong characteristics distinguishing it from *Avonia youngiana* but retaining several features, especially internally, which indicate a close relationship to that species. It is, therefore, assigned to the new subgenus *Quasiavonia*. *Quasiavonia* differs from *Overtonia* in being strongly lamellose on the pedicle valve, in the absence of prominent rugae, its finer spines and evenly concave brachial valve. The cardinalia are also distinct. *Krotovia* and *Levipustula* are not lamellose, have more densely arranged spines and less well defined dorsal adductor scars, while those of *Levipustula* are diamond-shaped (Muir-Wood & Cooper 1960, pl. 50, figs. 14, 15). The remaining genera, except *Avonia*, included within *Overtoniinae*, are all distinctive, and indeed, in some instances, bear little familial similarity e.g. *Rhytiophora* and *Stegacanthia*.

The new subgenus is included within *Avonia* because of similar dorsal interiors, similar transverse profiles, lamellose ornamentation and the tendency for *Quasiavonia* to show a slight ribbing on the flanks of adult valves. Differences are clear and sufficient to warrant supra-specific separation of the two. *Quasiavonia* reached a larger size than is known in well authenticated *Avonia* species; its shape is more rounded, the width remaining about the same as the length throughout growth. In *Avonia*, beyond about 8 mm. long, the length increased relatively more than the width. A faint ribbing is restricted to the antero-lateral valve margins of adult *Quasiavonia* shells and the concentric ornamentation is perhaps more strongly lamellose. But the strength of development of "growth lines" and lamellae is of less importance than other features and is commonly difficult to assess because of differences in preservation. A delicate ornamentation of lamellae is more readily preserved in an etched silicified fauna, such as that described here, than on specimens broken from solid rock, from which both ornamentation and the external shell layers may be removed. For this reason the type specimen may appear less spinose and ornamented than it was in life.

As *Avonia youngiana* does not occur in the Fermanagh fauna it has not been possible to make a statistical comparison of the two species.

Avonia* (*Quasiavonia*) *aculeata (Sowerby)

(Pl. 10, figs. 8–17; Pl. 11, figs. 1–21; Text-fig. 10)

1809 *Conchyliolithus Anomites* (*aculeatus*) Martin: 8, pl. 37, figs. 9, 10.
1814 *Productus aculeatus* Sowerby: 156, pl. 68, fig. 4.
1914 *Pustula aculeatus* (Martin) Thomas: 320, pl. 19, figs. 9, 10, ?11.
(See also for earlier references.)
1951 *Productus* (?*Krotovia*) *aculeatus* (Sowerby) Muir-Wood: 101, pl. 3, fig. 3.

DIAGNOSIS. Outline rounded quadrate to subcircular, width slightly greater than

length, umbo rounded, extending beyond straight hinge-line, cardinal extremities commonly perpendicular and flattened, maximum width at or near hinge-line; profile concavo-convex, nearly one-half as deep as wide; young with epithyrid pedicle sheath; concentric lamellae strongly developed over pedicle valve, less prominent on brachial valves; recumbent to suberect spines of about equal diameter arise posterior to each concentric lamella, short spine bases anteriorly and irregular radial arrangement; growth lines distinguishable; brachial valve with fewer and finer tapering spines; incipient ribbing slightly developed on adult flanks of both valves; ventral muscle field indistinct, adductor scars elongately trigonal to lanceolate, separated by narrow depression; diductor scars probably more rounded, spreading on to umbonal slopes; spine openings retained anteriorly; flattened to concave articulatory surfaces along hinge-line with slight ridges bounding postero-lateral region of visceral disc; cardinal process small, sessile with lobes distinctly separated posteriorly, supported by lateral ridges diverging from hinge-line at about 25° and extending towards postero-lateral margins; adductor scars smooth, raised and elongately trigonal, extending about one-quarter valve length; median septum weak between adductor scars and extending about two-fifths valve length; brachial impressions indistinct, lobate, at about 45° from mid-line, extending from antero-lateral margins of adductor scars for about two-thirds valve length; surface finely tuberculate.

MEASUREMENTS (in mm.):

	length	width
Shell (BB.52859)	15·2	15·4
Brachial valve (BB.52861)	10·5	15·0
Shell (BB.52862)	12·5	15·0
Shell (BB.52863)	8·0	8·7
Pedicle valve showing pedicle sheath (BB.52866)	1·6	1·8
Incomplete brachial valve (BB.52864)	3·5	c. 3·8
Brachial valve (BB.52865)	c. 4·5	5·5

LOCALITIES AND HORIZON. Subreefal limestones and shales. Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. Spines and lamellae were formed at all stages of growth, and while the lamellae became somewhat more widely separated anteriorly, the spines retained approximately the same density by the addition of further spines to each concentric row. On pedicle valves more than 5 mm. long, the spine separation in each row is about 1 mm., varying to 2 mm. medianly. Each spine arose obliquely from the shell surface, with a slight spine-ridge behind it, and continued to grow at about 40° or less to the valve, except for a row flanking the anterior border of the "ears", which grow at a higher angle and somewhat postero-laterally. On the brachial valve the spines are commonly tapered and towards the cardinal extremities the spines curve medianly over the valve (Pl. 11, fig. 1). Juvenile pedicle valves 1·5 mm. long have a supra-apical pedicle sheath protruding posteriorly from an oval protegulal node

about 0·2 mm. long. A shallow groove extends 0·4 mm. antero-ventrally from the protegulal node and is overhung by a pair of clasping spines 0·2 mm. apart (Pl. 11, figs. 9, 10). One further pair of clasping spines grew close to the hinge-line and about 1 mm. apart; however, these were preceded by the first two pairs of ordinary oblique spines which formed the first spine row at a valve length of about 0·7 mm. Up to a length of 3 to 4 mm. the spines grew fairly symmetrically in pairs, with the rare addition of a median spine, but the number in any one concentric band did not exceed four. Beyond this length additional spines were added so that a distinct radial pattern was produced. The spines were evidently of considerable length as one pedicle valve, 4 mm. long, has a spine 5 mm. long still remaining in position.

The lamellae and growth-lines indicate that shell shape remained fairly constant during growth. The curvature of the pedicle valve is regular while that of the brachial valve is less marked and tends to be slightly flattened across the middle of the visceral disc. In specimens longer than about 8 mm., the lamellae bend laterally, near to the posterior margin, forming small ears at the cardinal extremities. However, more rapid growth anterior to this restricted the formation of acutely angled ears and maintained the greatest width at a point commonly just anterior of the hinge-line (Pl. 11, fig. 4).

In common with many Overtoniinae, the ventral interior is poorly developed. The adductor scars are elongately trigonal to lanceolate markings about two-fifths as wide as long, extending from the beak for about one-third of the valve's length. The strong curvature of the umbonal region apparently led to a continued migration of the adductor bases anteriorly, so that these muscles would have had a more direct pull to their dorsal areas of attachment. This migration prevented the development of strongly marked scars. The same was probably true of the diductor muscle scars, which are wider than the adductor scars and spread on to the umbonal slopes. The

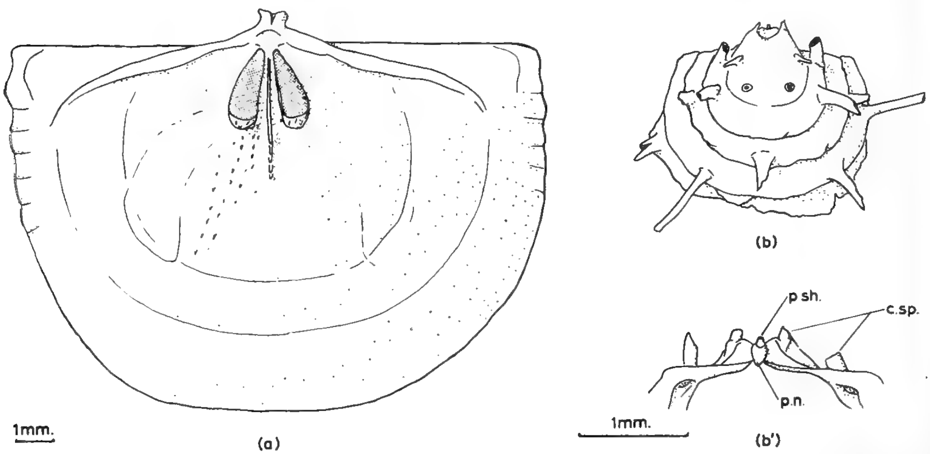

Fig. 10. Illustrations of the brachial valve interior (a), and a young pedicle valve viewed ventrally (b) and dorsally (b′) of *Avonia* (*Quasiavonia*) *aculeata* (J. Sowerby) *p.sh*, pedicle sheath; *c.sp*, clasping spine bases; *p.n*, protegulal node of the pedicle valve.

cardinal process of young valves, up to about 5 mm. long, is distinctly bilobed, the two lobes remaining separated by a deep groove posteriorly, but beyond this length the groove became less distinct and although the divergence of the myophores continued, at about 35°, secondary shell filled most of the intervening space. At the same time the lateral ridges grew posteriorly along the flanks of the cardinal process so that in the adult shell they extend well beyond the hinge-line (Pl. 10, fig. 13) The posterior margins of these ridges evidently articulated against the flattened to concave areas along the ventral hinge-line, which are anteriorly enclosed by slight ridges diverging across the inner margins of the ears from just inside the ventral umbo (Pl. 11, fig. 8).

The dorsal adductor scars are commonly distinguishable in valves 3 mm. long and extend for 1 mm. in length and slightly less in width. However, during growth their length, proportional to that of the valve, decreased, so that in valves about 10 mm. long the adductor scars are only one-quarter of this length (Pl. 11, fig. 16). At the same time the width of the adductor field grew to be rather greater than its length. Although the scars are well separated medianly, the median septum did not begin to form until valves were at least 5 mm. long. Thereafter its growth remained constant at about two-fifths of the valve length.

Several shells, both pedicle and brachial valves, have holes bored of about 0·5 mm. in diameter and these are thought to have been made by carnivorous gastropods.

TABLE 18

$\bar{L}$ mm. (var.) = 5·70 (15·499)	$\bar{L}$ mm. (var.) = 5·70 (15·499)
$\bar{W}$ mm. (var.) = 6·10 (19·637)	$\overline{Th}$ mm. (var.) = 2·70 (4·677)
r = 0·987	r = 0·895
a (var.) = 1·128 (0·00173)	a (var.) = 0·549 (0·00316)

TABLE 18. Statistics of length (L), maximum width (W) and thickness (Th) of 21 pedicle valves of A. (*Quasiavonia*) *aculeata* (*Sowerby*).

Genus ***KROTOVIA*** Fredericks 1928

1928 *Krotovia* Fredericks : 779, 790.
1952 *Krotovia* Fredericks ; Sarycheva & Sokolskaja : 92.
1960 *Krotovia* Fredericks ; Muir-Wood & Cooper : 188.

EMENDED DIAGNOSIS. Subcircular, width commonly slightly greater than length, hinge-line straight, more than one-half maximum width, venter rounded umbo prominent and extending beyond hinge-line ; strongly concavo-convex, about one-half as deep as long, body cavity narrow ; concentric ornamentation of growth lines and rare poorly developed lamellae ; fine suberect spines from small rounded tubercles with variably developed quincuncial arrangement ; umbonal slopes and cardinal extremities with weak irregular rugation ; brachial valve similar but also dimpled ; ventral adductor scars elongately trigonal, diductor scars elongately pear-shaped, extending beyond adductor scars on to umbonal slopes ; spines commonly retaining

internal openings ; cardinal process small, sessile, lobes well separated posteriorly and narrowly incised ; lateral ridges supporting process, extending posteriorly of hinge-line and anteriorly diverging from it at 20° to 30° towards postero-lateral margins, rarely extended as marginal ridge ; adductor scars ill-defined, elongately trigonal, postero-ventrally directed ; median septum poorly developed, about one-third valve length ; tuberculate.

Type species. *Productus spinulosus* J. Sowerby 1814, by original designation of Fredericks (1928).

Discussion. The genus was briefly defined by Frederick (1928) and redescribed by Muir-Wood & Cooper (1960 : 188), but as the internal characteristics of the type species, *P. spinulosus*, were then unrecorded, their description of the interiors was based upon *P. wallacianus* Derby, from the Lower Pennsylvanian of Brazil. The genus has much in common with *Avonia*, the new subgenus *Quasiavonia*, *Overtonia* and *Levipustula* of the Overtoniinae Muir-Wood & Cooper. It is distinguished from them by its lack of a differentiated concentric ornament in the form of rugae, strong lamellae or grouped and banded spines, and from *Levipustula*, in particular, in not having elongate spine bases, its weaker median septum and differently shaped adductor scars (cf. *Levipustula* Muir-Wood & Cooper 1960, pl. 50, fig. 15). The dorsal muscle scars of *Krotovia* are commonly less well developed than those of other genera within the subfamily.

Although commonly described as having a smooth surface, this is not entirely true, for apart from the development of incipient rugation towards the posterior margins of both valves, growth lines are occasionally accentuated as subdued lamellae.

Each spine is swollen at its base, so that shells from which the spines have been broken are ornamented by low rounded tubercles. These may be worn from abraded shells leaving a characteristic pattern of holes. The spines themselves are at a high angle to the shell, commonly at about 80°, delicate and all of much the same size. The quincuncial pattern is commonly best developed posteriorly, the spines antero-medianly being more widely spaced and less regular. Towards the adult anterior margin the spines tend to form more regular, closely arranged concentric rows.

Krotovia spinulosa (J. Sowerby)

(Pl. 12, figs. 1–18 ; Pl. 13, figs. 1–7)

1814 *Productus spinulosus* J. Sowerby : 155, pl. 68, fig. 3.
1861 *Productus spinulosus* J. Sowerby ; Davidson : 175, pl. 34, figs. 18–21.
1914 *Pustula spinulosa* (J. Sowerby) Thomas : 314, pl. 18, figs. 7–9, pl. 19, fig. 7, *non* fig. 8.
1928 *Krotovia spinulosa* (J. Sowerby) Fredericks : 779, 790.
1952 *Krotovia spinulosa* (J. Sowerby) ; Sarycheva & Sokolskaja : 92, pl. 14, fig. 98.

Emended diagnosis. Outline subcircular, width slightly greater than length, hinge-line about five-sixths maximum width, cardinal extremities commonly perpendicular ; profile strongly concavo-convex, nearly one-half as deep as long ; shell surfaces more or less smooth with sporadic development of lamellae and distinct

growth lines ; spines uniform in size, fine suberect at about 80° to surface, arising from quincuncially arranged low tubercles, about four in width of 2·5 mm., 5 mm. antero-medianly from ventral umbo ; umbonal slopes and cardinal extremities with incipient rugation ; adult anterior venter vaguely ribbed ; brachial valve similar but dimpled surface ; ventral adductor field about one-fifth valve length, anteriorly directed ; diductor scars extending beyond adductor scars, poorly defined ; cardinal process lobes deeply but narrowly incised dorsally, internally with pair of nodes at lobe bases, anterior to which strong lateral ridges cross and diverge from hinge-line at about 30° ; lateral ridges commonly terminating towards postero-lateral margins, rarely continued as circumvisceral ridge ; adductor scars commonly invisible, elongately trigonal, slightly raised and about one-fifth valve length ; median septum rarely developed, thread-like and about one-third valve length ; surface finely tuberculate, brachial markings indistinguishable.

MEASUREMENTS (in mm.) :

	length	width
Complete shell (BB.52867)	13·7	14·9
Complete shell (BB.52868)	6·8	7·5
Pedicle valve (BB.52869)	7·0	—
Pedicle valve (BB.52870)	4·4	4·1
Brachial valve (BB.52871)	7·8	9·6
Incomplete brachial valve (BB.52875)	6·0	*c.* 7·4
Complete brachial valve (BB.52874)	1·4	1·5
Complete shell (BB.52876)	14·8	16·0

LOCALITIES AND HORIZON. Subreefal limestones and shales, Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh, and Dockra limestone (BB.52876–77), Cunningham Baidland, Ayrshire, D_1.

Krotovia lamellosa sp.n.

(Pls. 13, figs. 8–16 ; Pl. 14, figs. 1–19)

DIAGNOSIS. Subcircular, concavo-convex *Krotovia* of same shape as type species ; concentric ornamentation of growth lines, well developed lamellae and spine rows, spines suberect to recumbent anteriorly, slight quincuncial pattern and spines of different sizes within each interlamellose band ; internally like type species, but perhaps more distinctly developed adductor scars and median septum.

MEASUREMENTS (in mm.) :

	length	width
HOLOTYPE. Complete shell (BB.52878)	9·0	10·1

		length	width
PARATYPES.	Complete pedicle valve (BB.52879)	9·1	9·6
	Incomplete pedicle valve showing ornament (BB.52880)	7·6	8·1
	Incomplete pedicle valve (BB.52881)	7·5	—
	Incomplete young pedicle valve (BB.52888)	2·1	—
	Complete pedicle valve (BB.52889)	1·8	1·9
	Complete brachial valve (BB.52883)	5·7	7·0
	Incomplete brachial valve (BB.52884)	7·3	—
	Complete brachial valve (BB.52885)	4·2	4·6
	Complete brachial valve (BB.52886)	4·1	4·6
	Incomplete brachial valve (BB.52887)	3·1	—

DISCUSSION. The external form and characteristics of *K. spinulosa* were re-described in detail by Thomas (1914 : 314), and from this, and other works, there seems little doubt that the present material is conspecific, and of use, therefore, in the emendation of both the genus *Krotovia* and the type species itself. Previously the internal characteristics of *K. spinulosa* were unrecorded, and while those of the present material are poorly impressed, they do, nevertheless, generally accord with those described for *Productus wallacianus* Derby by Muir-Wood & Cooper (1960 : 188). Although dorsal valves of the size (about 15 mm.) illustrated by these authors (pl. 50, fig. 11) are not available, it does seem that the cardinalia were less well developed than in *P. wallacianus*. However, despite their description of the dorsal adductor scars being " elongate subquadrate in outline ", the plate figure shows them to be the same shape as those of *K. spinulosa* i.e. elongately trigonal. The cardinal process is described as having a " minute median lobe posteriorly developed ", such a structure is not present in *K. spinulosa*. The two lobes of the cardinal process diverged at about 40° from one another throughout their development, as seen dorso-posteriorly, and retained a distinct cleft distally. Each lobe was deeply incised for the reception of the diductor muscles, and their enclosing ridges occasionally grew to such an extent as almost to surround the muscle bases. As growth proceeded the median pair of ridges, bordering the muscle bases, grew closer together at their proximal end, i.e. at the exterior base of the cardinal process, so that in adult valves these ridges are adjacent for one-half their length, before curving outwards to the distal tips of the lobes (Pl. 12, fig. 17). It could be that in poorly preserved material this basal region, where the median ridges are adjacent, may simulate a solid secondarily developed ridge. The primary positions of the tips of the lobes are commonly marked, in older valves, by a pair of nodes on the basal, ventral surface of the cardinal process (Pl. 12, fig. 18), growth having been by the addition of shell laterally and dorso-posteriorly.

The lateral ridges were strongly developed throughout growth, being distinguishable in brachial valves about 1 mm. long. In valves about 5 mm. long, their median ends had extended beyond the hinge-line, along the lateral flanks of the cardinal

process, while their lateral extremities commonly merged into one of the poorly defined concentric rows of internal tubercles. The valve length at which the adductor scars developed is very variable, but they can be seen rarely at this stage of growth (Pl. 12, fig. 13).

The spines are more or less regularly spaced over the two valves. Each spine has a rather swollen base, and these show as rounded tubercles in shells from which the spines have been broken. Towards the anterior margin of adult pedicle valves, more than 12 mm. long, the spine bases are somewhat elongate and contribute to a faint and irregular " ribbing ". This resembles *Overtonia* in that the incipient rib commonly continues anteriorly only to a point between the pair of anteriorly placed spines and then is lost. The spines are directed at a high angle from the valves but tend to curve ventrally, so that those placed on the lateral flanks of the pedicle valve may be at only about 40° to the surface. On the brachial valve the spines towards the postero-lateral margins curve antero-medianly.

The characteristic quincuncial pattern of spines on *K. spinulosa* is best developed over the posterior part of the shell, particularly within the first 7 to 8 mm. It is commonly lost antero-medianly because of a wider spacing of the spines in this region. However, some specimens, with particularly smooth surfaces, retain the regular pattern throughout a length of 15 mm. The occasional development of a lamella disrupts the pattern and commonly is followed by a rather more closely spaced concentric row of spines, having a modal value of 5 spines in 2·5 mm. width. Table 20 (A) gives the spine distribution. The tendency towards irregularity of this spine pattern is more marked in specimens from Co. Fermanagh than some collected from the Dockra limestone of Aryshire, and these latter shells have less frequently developed incipient lamellae.

The fauna from Co. Fermanagh contains approximately equal numbers of specimens of *K. spinulosa* and *Krotovia lamellosa* sp. nov. The taxonomic position of the latter is uncertain, and they may be merely lamellose varieties of *K. spinulosa*. The shells of *Krotovia lamellosa* are of the same shape as those of *K. spinulosa*, there being no significant difference between their lengths as compared to maximum widths or thickness ($P > 0{\cdot}5$). The only distinction made, at present, is in the form of the external ornamentation ; that of *Krotovia lamellosa* being clearly lamellose and with spines more obviously concentrically arranged. The spines do not have the same basal swellings as those of *K. spinulosa*, and are not all of the same diameter, although there is an indistinct quincuncial pattern.

The frequencies of the spines in the two species are set out in Table 20. Pedicle valves more than 5 mm. long commonly lose the quincuncial pattern and between the lamellae the spines are arranged in irregular bands with those more anteriorly placed having a slightly smaller diameter and placed radially between the posterior ones. In this way the interlamellose bands may have up to three ranks of spines, and this in itself gives a local diagonal pattern (Pl. 13, fig. 11). This is reminiscent of the arrangement on members of the Echinoconchinae, but those shells contrast with the present material in having almost flat brachial valves and different interiors. The grouping of spines into interlamellose bands is only sporadically developed and

probably the two features are linked, in other words the formation of a lamella inhibited spine growth for a short period, after which the spines were more crowded than usual until the formation of the next lamella. Indeed, it could be argued that *Krotovia lamellosa* is *K. spinulosa* in which lamellae have been more strongly developed than is usual. However, gradational forms are not found in the fauna so the external differences are considered to be valid specific characteristics, and there is a tendency for the lateral ridges to be less divergent and the dorsal adductor scars better developed in *K. lamellosa* than in *K. spinulosa*.

Despite the ventral beaks commonly having been broken in these shells, it is possible to collect material showing a minute pedicle sheath, about 0·03 mm. in diameter, ventral to which is the usual shallow groove. In common with other juvenile productoid shells, there are usually two pairs of clasping spines that curve posteriorly over the beak and probably assisted in the attachment of the young shells.

TABLE 19

	A	B
$\bar{L}$ mm. (var. L.)	7·07 (13·246)	5·94 (4·998)
$\overline{Th}$. mm. (var. Th.)	3·28 (4·120)	2·89 (1·529)
r	0·989	0·988
$Log_e\ \bar{L}$ (var. Log_e L)	1·837 (0·2382)	1·716 (0·1328)
$Log_e\ \overline{Th}$ (var. Log_e Th)	1·024 (0·3243)	0·893 (0·1681)
r_e	0·995	0·996
α (var. α)	1·666 (0·00005)	1·2335 (0·0005)

TABLE 19. Statistics of length (L) and thickness (Th) of 30 shells and pedicle valves of *Krotovia spinulosa* (J. Sowerby) (A), and 21 shells and pedicle valves of *Krotovia lamellosa* sp. n. (B).

TABLE 20

	A				B		
No. of spines	3	4	5	6	4	5	6
At 5 mm.	1	14	9	1	5	10	5
At 10 mm.	4	3	0	0	0	0	0

TABLE 20. The number of spines counted in a width of 2·5 mm. at a distance of 5 mm. and 10 mm. antero-medianly from the ventral umbo of *Krotovia spinulosa* (J. Sowerby) (A), and *Krotovia lamellosa* sp. n. (B).

Family **MARGINIFERIDAE** Stehli 1954

Subfamily **MARGINIFERINAE** Stehli 1954

Genus ***EOMARGINIFERA*** Muir-Wood 1930 : 103

TYPE SPECIES. *Productus longispinus* J. Sowerby, by original designation of Muir-Wood (1930 : 103).

DISCUSSION. *Eomarginifera* was erected in 1930 to include small quadrate shells with ribs developed throughout life ; six symmetrically arranged spines on the pedicle valve ; lamellose thickenings around the brachial valve margins and with poorly developed internal marginal ridges. In addition to the type species, Muir-Wood included *Productus derbiensis* Muir-Wood, *P. lobatus* J. Sowerby, *P. minutus* Muir-Wood, *P. praecursor* Muir-Wood, *P. pseudoplicatilis* Muir-Wood, *P. setosus* Phillips, *P. tissingtonensis* Sibly and *P. triquetrus* Muir-Wood, in *Eomarginifera*. Of these forms *P. minutus* and *P. triquetrus* have since been tentatively assigned to *Alifera* by Muir-Wood & Cooper (1960). These authors did not assign *P. pseudoplicatilis*, which has here been included in *Plicatifera* (see p. 204). *P. tissingtonensis* was also left unplaced, although it is referred to *Eomarginifera* in the text (1960 : 220).

There is a proliferation of species within *Eomarginifera* and related genera, showing considerable variation and the complete group warrants a thorough reinvestigation. Unfortunately, such a study is beyond the scope of the present work. Meanwhile all that can be said is that specimens at present assigned to *Alifera panderi* (= *P. minutus*) include some belonging to the new subgenus *Eomarginiferina* (e.g. some specimens in the British Museum (Natural History) from Little Island, Cork and from Derbyshire), and that *Eomarginifera* Muir-Wood 1930 appears to include large coarsely ribbed forms like *E. lobata* and smaller shells with either wide or narrow ribbing, such as *A. panderi* and *E. longispina* respectively. The presence or absence of major spines on the hinge-line may prove to be of diagnostic value. Such spines are never found on the newly described Fermanagh valves.

By including *Eomarginiferina* as a new subgenus of *Eomarginifera* it is necessary to emend the generic description given by Muir-Wood & Cooper (1960 : 209) with regard to the spines and the pedicle valve interior. The pedicle valve ornamentation must include : juvenile spines or spine-bases posteriorly confined, major spines symmetrically arranged, commonly in threes, near cardinal extremities, on umbonal slopes and on anterior venter. Interior of pedicle valve commonly traversed by prominent ridges corresponding to rib interspaces and extending to trail, lobate diductor scars enclosing elongate-oval adductor scars posteriorly confined ; marginal ridge rarely developed.

Subgenus ***EOMARGINIFERINA*** nov.

1930 *Eomarginifera* Muir-Wood : 103 (pars).
1960 *Alifera* Muir-Wood & Cooper : 207 (pars).

DIAGNOSIS. Outline subrounded with flattened triangular ears at greatest width

of shell, adult anterior margin commonly extended by low fold ; profile subhemispherical, concavo-convex, bachial valve gently concave across visceral disc but strongly curved anteriorly forming short trail, body cavity moderately deep ; radial ornament of low rounded costae, with rare bifurcations, forming reticulate pattern over visceral regions through intersection with rounded persistent rugae ; spines confined to pedicle valve, three strong cylindrical spines, one pair laterally directed from each umbonal slope, single median spine slightly anterior of rugate region ; young with pedicle sheath, clasping spines and small spines arranged on rugae umbonally ; internally ventral visceral region traversed by strong ridges corresponding to rib interspaces and with additions by intercalation corresponding to external bifurcations, ridges posteriorly flattened by flabellate diductor field, anteriorly irregularly spinose ; ears strongly demarcated by ridges curving from near hinge-line ; three principal spines retain internal openings and rimmed by secondary shell ; cardinal process squat, lobes separated internally by shallow groove, fused posteriorly, supported by lateral ridges that diverge from hinge-line and continue round inside of ears as strong ridges, commonly dying out around antero-lateral margins ; adductor scars smooth, divisible into raised subtrigonal anterior scars and irregular oval posterior scars ; low thickened ridge connects base of cardinal process to anterior adductor scars ; median septum low between scars, narrow but high anteriorly, extending to about mid-length of valve ; brachial ridges lobate to reniform with antero-lateral raised areas ; strong anteriorly directed tubercles on anterior region of disc, finely tuberculate elsewhere.

Type species. *Eomarginifera* (*Eomarginiferina*) *trispina* subgen. et sp. n.

Discussion. The subgenus is typically marginiferid in its small size, rather globose profile and few symmetrically arranged spines. But it does not agree in the marginiferinid characteristic of having a " brachial interior with a marginal ridge bounding the visceral disc " (Stehli 1954 : 321). In this respect the genus is reminiscent of the Costispiniferae, members of which have " crenulated ridges extending across the ears of both valves ; prominent endospines in row anterior of septum " (Muir-Wood & Cooper 1960 : 217). However, in other characteristics the genus is quite unlike those included under the Costispiniferae but similar to those of the Marginiferinae, the subfamily under which *Eomarginiferina* is here assigned. Because of this anomaly it is desirable to redefine these subfamilies and the following emended diagnoses are suggested : Marginiferinae. Marginiferidae commonly with continuous externally crenulated, marginal or submarginal ridges around viceral disc of brachial valve externally free of spines. Costispiniferinae : Marginiferidae with crenulated ridges across ears of both valves ; prominent endospines anterior to brachial impressions and both valves typically externally spinose. The genera included by Muir-Wood & Cooper (1960 : 205) within the Marginiferinae, with the exception of some *Eomarginifera* species, commonly have an antero-ventral sulcus. Two-thirds of the adult specimens of *Eomarginiferina* have a low antero-median fold ; no specimens are sulcate. There is a consistent development of three strong spines, arranged symmetrically at about the same growth stage in a manner quite unlike

other described genera. Certain specimens of *Alifera panderi* Muir-Wood & Cooper 1960 have three spines similarly arranged, and although described as having "six major spine bases" (Muir-Wood 1928 : 195) they may prove to be congeneric, if not conspecific with *Eomarginiferina trispina*.

The morphology of the subgenus is most closely related to *Eomarginifera* and *Alifera*. It differs from the former in its folded anterior margin, spine arrangement, smaller adult size and different dorsal adductor scars. *Eomarginiferina* differs from *Alifera* in not being anteriorly sulcate; in having fewer rugae; a different spine arrangement; in its lack of a ventral marginal rim, and in its dorsal interior. It appears from pl. 66, figs. 13 and 17 (Muir-Wood & Cooper 1960) that the ventral interiors may have been similarly ridged and spinose (cf. Pl. 16, fig. 18).

The ventral interior of *Eomarginifera* is described by Muir-Wood & Cooper as having "flabellate diductor scars" that extend "to the end of the visceral disc". It is unlikely, however, that the diductor scars could have extended to the anterior margin of the visceral disc of this genus and still have left room for the important brachial cavity. The brachial scars of the genus are suggestive of a well formed lophophore hanging into an open brachial cavity. Pedicle valve interiors of type material of *Eomarginifera* are poorly represented, but it is suggested that the diductor scars of Muir-Wood & Cooper may be the prominent ridges of *Eomarginiferina*, which are fully described under *E. trispina*. It is relevant to note that etched specimens of eomarginiferids studied by the author and collected from linestones of D. age from Cunningham Baidland, Ayrshire, do possess similar ridges to those of *Eomarginiferina*, and also show well developed posteriorly placed adductor and diductor scars.

Until such time as a full revision of *Eomarginifera* and related genera is undertaken, *Eomarginiferina* is retained as a subgenus, but some species presently ascribed to *Eomarginifera* or *Alifera* may well belong within this species group, and necessitate its elevation to generic rank.

Eomarginifera* (*Eomarginifera*) *trispina subgen. et sp.n.

(Pls. 15, figs. 9–22; Pl. 16, figs. 1–22; Text-fig. 11)

?1928 *Productus minutus* Muir-Wood : 195, (pars), *non* pl. 12, fig. 3.

Diagnosis. Outline subrounded, greatest width at or equal to straight hinge-line, length about five-sixths maximum width, ears commonly prominent and demarcated from umbonal slopes by shallow groove; profile subhemispherical with slight geniculation at deepest part of valve, greatest thickness about two-thirds length; body cavity about two-ninths shell length; short antero-dorsally directed trail, commonly with slight median fold; multicostellate, ribs low, rounded and persistent, six in 2·5 mm. at 5 mm. antero-medianly of ventral umbo; nine or ten rugae, commonly persistent, rounded and increasing in width anteriorly; pedicle valve sparsely spinose, typically with three strong erect spines arising symmetrically and nearly concentrically, pair on umbonal slopes projecting laterally beyond cardinal extremities and single one projecting antero-ventrally from mid-valve, anterior of

rugation ; small sub-erect spines on first 3 mm. from umbo, arising from intersections of costae and rugae ; ventral interior traversed by strong spinose ridges corresponding to intercostal spaces, spinose nature prominent anteriorly, ridges flattened and indistinct posteriorly, in region of indistinct small median adductor scars and flabellate diductor scars ; ears strongly demarcated ; cardinal process with short shaft, lobes internally divergent and separated by shallow groove, myophores posteriorly directed ; lateral ridges diverge from hinge-line at about 20° for about two-thirds hinge width, continue around insides of ears as strong externally crenulated ridges ; adductor scars smooth, anterior scars raised, subtrigonal, posterior scars irregularly rectangular, both surrounded by secondary shell in adult valves, about one-quarter valve length ; median septum narrow, low between adductor scars and posteriorly buried in secondary shell forming low broad, medianly grooved ridge to base of cardinal process ; septum high anteriorly and extending about one-half valve length ; postero-lateral brachial ridges from near junctions of anterior and posterior adductor scars, at about 60° to mid-line, extending about five-eighths valve length and forming lobate to reniform impressions enclosing thickened areas antero-laterally ; anteriorly directed spine-like tubercles irregularly arranged radially and concentrically.

Measurements (in mm.) :		length	width
Holotype :	Complete shell (BB.52890)	8·2	*c.* 10·4
Paratypes :	Complete shell (BB.52891)	9·0	8·5
	Complete pedicle valve (BB.52892)	9·0	8·3
	Pedicle valve (BB.52893)	9·5	10·7
	Pedicle valve (BB.52894)	9·5	8·5
	Incomplete shell (BB.52903)	*c.* 9·0	11·8
	Brachial valve (BB.52895)	8·0	10·0
	Brachial valve (BB.52896)	5·0	7·5
	Brachial valve (BB.52897)	7·0	6·8
	Incomplete pedicle valve, to show spine pattern (BB.52898)	6·7	9·2
	Incomplete shell with juvenile spines (BB.52899)	6·5	8·3
	Juvenile pedicle valve showing pedicle sheath (BB.52900)	3·2	3·6

Localities and horizon. Subreefal argillaceous limestones of Carrick and Bunnahone Loughs, and rarely in reef breccias of Knockmore, near Derrygonnelly, Co. Fermanagh. D_1.

Discussion. The species is characterized by its small size, three symmetrically placed major spines and common development of a slight fold in the trail of adult

pedicle valves. This fold is associated with a shallow V-shaped extension to the median part of the trail, although the brachial valve remains unfolded.

The two lateral spines are placed below the ears, close to their junctions with the umbonal slopes, and extend more or less laterally. They are set about five-sixths of the body width from each other and on the anterior ruga. The median spine is placed at about three-fifths of the valve length, measured from the hinge-line, a little anterior of the anterior ruga, commonly on one of the radial ribs, and is antero-ventrally directed. The growth of these three spines occurred at a similar stage of development, and one at which the brachial valve curved strongly against the pedicle valve to form the trail. Prior to this, the strong curvature in the growth of the pedicle valve must have caused the anterior commissure to rotate antero-dorsally relative to the surface of the substratum. It is postulated, therefore, that the small spines scattered over the first 2 to 3 mm. of the pedicle valve helped to anchor the young shell, while at adulthood, when the relative rotation of the brachial valve had ceased, the three major spines grew and in so doing helped to maintain the position of the shell. In 5 out of about 200 pedicle valves the median spine is replaced by two closely, but irregularly, situated spines. Such valves are considered as freaks and the duplication may have resulted from damage. On the other hand it could be a sign of the tendency for the growth of additional spines, seen more fully developed in the previously established genera of the Marginiferidae.

The adult radial ornament is distinguishable over the complete shell. Bifurcations of the costae are rare, but several commonly occur at the same growth stage. The costation is more persistent than the rugation and 5, 15, and 8 valves have 5, 6 and 7 ribs in 2·5 mm., 5 mm. antero-medianly of the ventral umbo. The ribbing is less clearly distinguishable on young shells and posteriorly.

The strong radial ridges inside the pedicle valve occur along the interspaces of the

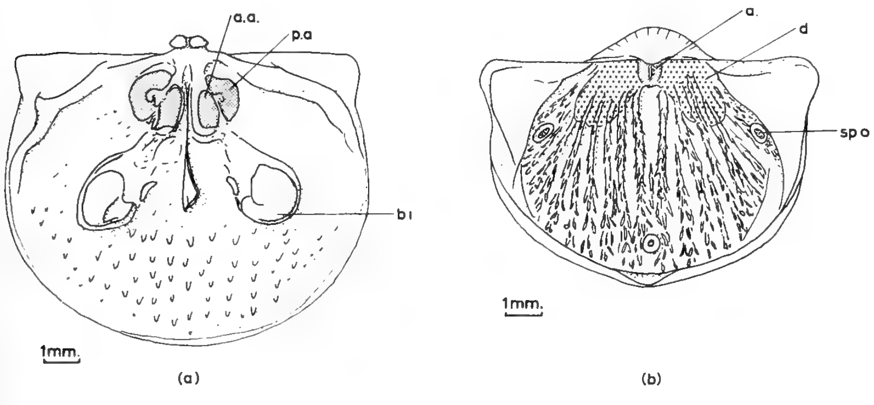

FIG. 11. Illustrations of (a) the brachial valve interior and (b) the pedicle valve interior of *Eomarginifera* (*Eomarginiferina*) *trispina* sp. n. to show the internal morphology; *a.a*, anterior adductor scars; *p.a*, posterior adductor scars; *b.i*, brachial impressions; *a*, adductor scars; *d*, diductor scars; *sp.o*, spine opening.

costellation, so that a bifurcation of a rib is represented internally by the intercalation of an additional ridge. The ventral interior is almost smooth posteriorly, except for a slight median ridge which probably separated the adductor scars (Text-fig. 11, b). The strong radial ridges extend anteriorly from the smooth region over the complete visceral surface, to the point where the brachial valve geniculated against the pedicle valve, i.e. to about the position of the opening of the single antero-median spine. Towards their anterior ends the ridges become increasingly tangled by a complex of more or less anteriorly directed spinose tubercles (Pl. 16, fig. 18). However, the connections to the lateral spines, and commonly to that of the antero-median spine remained open allowing the continued life of those spines, even after the development of the tuberculate ridges had surrounded them (Pl. 16, fig. 22). A study of a growth series of ventral interiors reveals that these ridges only developed when the shell had almost fully grown, and they became increasingly prominent with age. The development of the spinose tubercles on the ridges anteriorly was followed by the break down of the ridges themselves leaving only the spinose mass over the anterior one-half of the visceral region. At the same time flattening and resorption of these ridges occurred posteriorly producing flabellate areas considered to be the diductor scars, which extended about 3 mm. from the beak. The intimate relationship between internal and external ribbing, together with its extension over the complete visceral interior, precludes the possibility that these ridges were the attachment areas for the diductor muscles. Their position and development suggests that they were formed as a result of an extensive and closely pinnate mantle canal system, and in all probability represent the ridges between the gonocoel canals. Hence their late development, at sexual maturity, followed by the anterior break down of the ridges as the gonadal strands increased in size, and the tubercles which retained the mantle muscle strands which assisted in the circulation and expulsion of the gonadal products. The rudimentary mantle canals were outward folds of the mantle and these controlled the external radial ornament. A dichotomy of the mantle canal occurred during the bifurcation of the rib, while internally shell deposition between the canals produced the ridges and intercalations between the canal branches.

A closely comparable development of ridges between the gonocoels of *Alifera konincki* Muir-Wood & Cooper are illustrated by these authors (1960, pl. 66, figs. 6, 8, 13, 16, 17) on internal moulds, but are not mentioned in the text where the " subflabellate diductor scars " are mistakenly described as " not enclosing adductor scars " (: 207). The dorsal interiors and form of the shells clearly distinguish these two species.

Spats of *E. trispina* were probably attached during their early development by a pedicle which extruded through a small posteriorly directed pedicle sheath (Pl. 16, figs. 3, 4). In common with several other productacean genera, the brephic valve was shallowly grooved, perhaps through some bipartite development inherited from the larval stage, and was probably furnished with a pair of small encircling spines. Besides these spines, two pairs of clasping spines developed close to the hinge-line and about 1 mm. and 1·75 mm. apart. These spines curved ventro-posteriorly in

such a way as to have gripped any suitably placed object, and rarely were incurved to make contact with their own valve surface after which they continued to grow along the surface for some distance (Pl. 15, fig. 9). This behaviour indicates the way in which the growing spine must have been capable of altering its direction of growth, in response to solid objects, by the varied proliferation of columnar epithelium at the tip of the spine mantle tissue (Williams 1956 : 252). Fourteen to sixteen additional fine, suberect spines developed from the rugae in more or less symmetrical pairs, together with one or two medianly placed spines, over the first 2 or 3 mm. of the pedicle valve. No more spines were produced until the three major spines developed after a further growth of between 4 and 6 mm. (Text-fig. 4 a–c).

Ribbing and growth-lines are the sole ornamentation anterior of the median major spine. The rib immediately anterior of this spine may continue rather broader than the others, and along the trail forms the crest of the shallow median fold. This fold was seen in 34 out of 45 valves, and is rather variable in its form. Commonly from 1 to 3 mm. of the antero-dorsal margin of the pedicle valve are folded into a shallow V, but rarely the fold is less pronounced while the whole margin is extended more anteriorly than usual. A slight, but apparently similar fold is seen on *Eomarginifera praecursor* (Muir-Wood). The external form and costellation also seem similar, but the species differ in that *E. praecursor* has six major spines on the pedicle valve (Muir-Wood 1928 : 192). Unfortunately it has not been possible to compare internal characteristics.

Because of the high proportion of articulated shells, and the delicate nature of young brachial valves, it has not been possible to trace the development of the brachial valve throughout its growth. It is clear, however, that while the anterior adductor scars were slightly raised and clearly distinguishable for much of the shell's growth, the posterior adductor scars only became clearly differentiated in adulthood, by the development of surrounding secondary shell, and probably only after the trail had formed. The median septum was developed anteriorly, from between the adductor scars, and was always highest anteriorly. The low broad ridge from the base of the adult cardinal process and median ends of the lateral ridges which connect to the posterior ends of the anterior adductor scars, is made of secondary shell substance and developed at about the same time as the thickening around the posterior scars and the platforms within the brachial impressions. This posterior median ridge bifurcates close to the cardinal process with the formation of a shallow groove leading down to the depression between the anterior adductor scars, from which the median septum arises. The brachial impressions are distinguishable in valves with a visceral disc about 5 mm. long. But not until reaching a visceral length of about 6 mm. did the antero-lateral regions become strongly thickened. The lateral ridges were probably distinguishable medianly from an early stage, and the ridges demarcating the ears (" ear-baffles ") were certainly present when the valve was 5 mm. long. It was not until growth had continued beyond this length that the lateral ridges merged with the ear baffles as a continuous line of shell thickening. This pattern of growth is common to several productacean genera, e.g. *Plicatifera* and *Overtonia* (Text-fig. 5).

TABLE 21

$$\overline{\mathrm{L}}\ \text{mm. (var.)} = 7{\cdot}46\ (0{\cdot}367) \qquad \overline{\mathrm{SpL}}\ \text{mm. (var.)} = 4{\cdot}53\ (0{\cdot}313)$$
$$\overline{\mathrm{W}}\ \text{mm. (var.)} = 8{\cdot}72\ (0{\cdot}144) \qquad \overline{\mathrm{SpW}}\ \text{mm. (var.)} = 7{\cdot}18\ (0{\cdot}203)$$

TABLE 21. Statistics of length (L.), width (W), the distance from the umbo to the median major spine (Sp L), and the distance between the lateral pair of spines (SpW) of 20 adult pedicle valves of *E.* (*Eomarginiferina*) *trispina* sp. n.

TABLE 22

No. of rugae	8	9	10	11	12
No. of specimens	1	9	6	5	2

TABLE 22. The number of rugae counted across the visceral region of 23 pedicle valves of *E.* (*Eomarginiferina*) *trispina* sp. n.

TABLE 23

No. of ribs	5		6		7
No. of specimens	5	2	15	0	8

TABLE 23. The number of radial ribs counted in 2·5 mm. at a distance of 5 mm. anteromedianly from the umbo of 30 pedicle valves of *E.* (*Eomarginiferina*) *trispina* sp. n.

TABLE 24

$$\overline{\mathrm{L}}\ \text{mm. (var.)} = 6{\cdot}00\ (4{\cdot}096) \qquad \overline{\mathrm{L}}\,\mathrm{r}\ \text{mm. (var.)} = 4{\cdot}90\ (1{\cdot}481)$$
$$\overline{\mathrm{Th}}\ \text{mm. (var.)} = 2{\cdot}49\ (1{\cdot}949) \qquad \overline{\mathrm{Thr}}\ \text{mm. (var.)} = 1{\cdot}25\ (0{\cdot}181)$$
$$\mathrm{r} = 0{\cdot}961 \qquad \mathrm{r} = 0{\cdot}892$$
$$\mathrm{Log}_e\,\overline{\mathrm{L}}\ (\text{var. }\log_e \mathrm{L}) = 1{\cdot}738\ (0{\cdot}108) \qquad \mathrm{Log}_e\,\overline{\mathrm{Lr}}\ (\text{var. }\log_e \mathrm{Lr}) = 1{\cdot}559\ (0{\cdot}060)$$
$$\mathrm{Log}_e\,\overline{\mathrm{Th}}\ (\text{var. }\log_e \mathrm{Th}) = 0{\cdot}775\ (0{\cdot}274) \qquad \mathrm{Log}_e\,\overline{\mathrm{Thr}}\ (\text{var. }\log_e \mathrm{Thr}) = 0{\cdot}169\ (0{\cdot}109)$$
$$\mathrm{r}_e = 0{\cdot}972 \qquad \mathrm{r}_e = 0{\cdot}907$$
$$\alpha\ \text{(var.)} = 0{\cdot}5037\ (0{\cdot}000496) \qquad \alpha\ \text{(var.)} = 1{\cdot}348\ (0{\cdot}01146)$$

$$\overline{\mathrm{L}}\ \text{mm. (var.)} = 6{\cdot}00\ (4{\cdot}096)$$
$$\overline{\mathrm{W}}\ \text{mm. (var.)} = 7{\cdot}13\ (5{\cdot}335)$$
$$\mathrm{r} = 0{\cdot}968$$
$$\mathrm{a}\ \text{(var.)} = 1{\cdot}142\ (0{\cdot}00293)$$

TABLE 24. Statistics of length (L), maximum width (W), thickness (Th), length of rugate region (Lr), and thickness of rugate region (Thr) of 30 shells or pedicle valves of *E.* (*Eomarginiferina*) *trispina* sp. n.

Subfamily **ECHINOCONCHINAE** Stehli 1954

Genus ***ECHINOCONCHUS*** Weller 1914

Echinoconchus cf. ***punctatus*** (J. Sowerby)

(Pl. 17, figs. 11–15 ; Pl. 18, figs. 1–4)

MATERIAL. Few fragmentary remains from the Bunnahone locality near Derrygonnelly, Co. Fermanagh. D_1.

MEASUREMENTS (in mm.)

	length	width
Young pedicle valve (BB.52936)	—	15·5
Incomplete brachial valve (BB.52938)	1·6	—
Incomplete brachial valve (BB.52939)	*c.* 24·0	*c.* 29·0

DESCRIPTION. *Echinoconchus* is insufficiently represented in the faunas to allow a full description, but a few young valves identified as *Echinoconchus cf. punctatus* (J. Sowerby) are represented. The fragments are typical of the subfamily in having concentrically arranged bands of recumbent spines of more than one diameter. The spines are concentrated on anteriorly sublamellose rugae. The spines occur in up to 5 ranks in each concentric band and when all are preserved they form a dense anteriorly directed comb in which the lower, more anteriorly placed, spines are more slender. This feature, together with almost flat brachial valve and its interior, distinguishes the young valves of *Echinoconchus* from those of *Krotovia lamellosa* sp. n., with which it occurs in the Fermanagh faunas.

The dorsal interiors are described by Thomas (1914) and by Muir-Wood & Cooper (1960) as having lateral ridges that continue along the hinge margin. In the Fermanagh valves the lateral ridges diverge from the hinge margin and merge laterally into indistinct ridges formed at the interspace of two external rugae (Pl. 17, fig. 13). There are no interiors amongst Sowerby's original specimens, so while the descriptions of the above authors is probably inaccurate for young specimens, this difference may result only from the juvenile nature of the Fermanagh material in which secondary shell deposition along the hinge margin had not taken place. (A similar ontogenetic change occurred in *Plicatifera plicatilis*.)

Genus ***PUSTULA*** Thomas 1914

Pustula cf. ***pyxidiformis*** (de Koninck)

(Pl. 18, figs. 5–14 ; Pl. 19, figs. 1, 2)

MEASUREMENTS (in mm.)

	length	width
Incomplete pedicle valve (BB.52940)	36·0	—
Incomplete shell (BB.52941)	*c.* 33·0	*c.* 45·0
Incomplete shell (BB.52942)	*c.* 43·0	*c.* 60·0
Incomplete brachial valve (BB.52943)	31·4	42·5

The genus is poorly represented in the Bunnahone fauna by a few incomplete large specimens, and no young valves were found. For this reason a full description has not been attempted and the specimens are only tentatively assigned.

These shells, whigh are large for the fauna, are more or less plano-convex when adult; there is a short antero-dorsally directed trail and the pedicle valve is slightly medianly sulcate. The ornamentation is distinctive, consisting of poorly developed rugae, becoming sublamellose anteriorly, from between which more or less radially arranged prostrate spines arise from elongate spine bases having an irregular quincuncial pattern. The pedicle valve interior for *Pustula* was not described by Muir-Wood & Cooper (1960), so the available valve is noteworthy (Pl. 18, figs. 5–7). The muscle field extends about two-thirds of the valve length (measured as a chord to the valve's curvature) and is clearly divisible into raised central adductor scars and flanking, longitudinally striated, elongately trigonal diductor scars. The median sulcation occurs most prominently in the anterior region of, and just anterior to, the adductor platform. The brachial valve has a short postero-dorsally directed cardinal process with trifid external surface, as a result of fusion of the median muscle boundaries. Internally it is supported by the low posterior end of the median septum and a pair of well developed lateral ridges that diverge from the hinge-line at about 10° and extend for about three-quarters of the hinge width. The muscle and brachial impressions are obscure or lacking in the present material, but are poorly known from specimens of other areas.

The taxonomic position of these Fermanagh specimens is in doubt as their dorsal interiors are more comparable to the American genus *Stegacanthia*, as illustrated by Muir-Wood & Cooper (1960, pl. 48, fig. 12), than to *Pustula* (pl. 84, fig. 4) from the British Isles. For the present and until further material can be collected from Ireland and compared with American species, the Fermanagh shells are questionably assigned to *P. pyxidiformis* solely by reason of their comparable external ornamentation. The ornamentation of the holotype of *Pustula pustulosa* (B.M.N.H. no. B.419) is of more discrete pustule-like spine bases confined to indistinct rugae, and only anteriorly do these spine bases become somewhat elongate, as is typically seen on *P. pyxidiformis* and *Stegacanthia bowsheri*.

Family **DICTYOCLOSTIDAE** Stehli 1954

Genus ***ANTIQUATONIA*** Miloradovich 1945

Antiquatonia sp.

(Pl. 17, figs. 1–10)

A well preserved incomplete pedicle valve, together with a few fragments of other pedicle valves from the Bunnahone locality, clearly show the characteristics of *Antiquatonia*. Brachial valves are not known for certain, but the fragment illustrated (Pl. 17, figs. 7–10), together with three other similar cardinalia, are thought to belong to the genus.

MEASUREMENTS (in mm.)	length	width
Incomplete pedicle valve (BB.52934)	25	c. 39

About 20 rugae are developed over the postero-ventral part of the pedicle valve but the anterior 4 or 5 are not persistent and die out across the slightly sulcate median region. The ribbing is well developed with about 6 ribs occurring in 2·5 mm., 5 mm. antero-medianly of the ventral umbo. The ribs continue on the trail but are not of uniform width, possibly as a result of spine-growth interference. Two pairs of prominent rows of spines are developed ; one pair extending from near the umbo towards the postero-lateral margins, at a narrow angle to the hinge-line ; the other pair developed along the flanks, just below the groove that separates the ears from the flanks, and arose from a low ridge.

Internally the " rarely developed transverse ridges across the ears " (Muir-Wood & Cooper 1960 : 270) are present, as are the dendritic raised adductor scars and flabellate longitudinally striated diductor scars. Anterior to these, and covering the remainder of the inferred visceral cavity, are irregular ridges comparable to those observed in *E. Eomaginiferina* subgen. nov. (Pl. 17, fig. 3).

The fragment of brachial valve appears to be comparable to that known for *Antiquatonia*. The cardinal process is sessile and trifid, by the complete fusion of the median muscle boundary ridges, and each myophore is deeply incised. The lateral ridges do not appear to diverge from the hinge-line of the available specimens. The median septum is low and broad posteriorly, supporting the cardinal process, but between the adductor scars is poorly developed and anteriorly it is high and blade-like.

Family **LINOPRODUCTIDAE** Stehli 1954

Genus ***OVATIA*** Muir-Wood & Cooper 1960

Ovatia sp.

(Pl. 19, figs. 3–10)

A few silicified shells from the Bunnahone locality are ascribed to *Ovatia* although the genus was previously unrecorded from the British Isles (Muir-Wood & Cooper 1960 : 314). The remains are of young valves but indicate a subcircular outline, and the most prominent external ornamenation is of fine radial ribbing developed over both valves ; there being about 8 ribs in 2·5 mm., 5 mm. from either umbo. Costellae seem to be added by dichotomous branching on the brachial valve and by intercalation on the pedicle valve. Spines are developed from the ribs, expecially posteriorly (Pl. 19, fig. 10), and a small pedicle sheath was most probably present during early life. An indistinct rugation is most clearly developed laterally and posteriorly, near the straight hinge-line. The cardinal process is sessile and quadrifid, although the two median muscle boundaries are only narrowly separated (Pl. 19, fig. 4) and might well appear fused, giving a trifid process, in less well preserved material. Internally the median muscle boundaries extend beyond the lateral muscle bound-

aries and the cardinal process is supported by both the lateral ridges and a broad low median septum which becomes narrow and high anteriorly.

Measurements (in mm.)

	length	width
Incomplete pedicle valve (BB.52945)	c.6·0	7·4
Incomplete pedicle valve (BB.52946)	—	c. 8·0
Incomplete brachial valve (BB.52947)	c. 11·5	—

Although similar, *Cancrinella* Fredericks is more clearly rugate and the pedicle valve is more spinose, while *Linoproductus* Chao has a rather different dorsal interior. Both these species are restricted to Upper Carboniferous and Permian rocks by Muir-Wood & Cooper (1960 : 298, 302). It seems possible that the Fermanagh shells represent the young of forms precursory to true linoproductids of higher strata and that older rocks, down to the Ballyshannon Limestone, contain species of *Ovatia* or *Balakhonia* and not *Linoproductus* as commonly described in the past.

Recently Sarycheva (1963 : 231) described her new genus *Balakhonia* from the Visean to Namurian of the Kuznetsk Basin. This genus was erected for species commonly attributed to *Linoproductus*, but which differ internally and in having thin shells and a narrow body cavity. The cardinal process is described as being small and bilobed, the two lobes being separated and not fused medianly, as they are in the heavy trifid cardinal process of *Linoproductus*. Spines are neither prominent nor frequent on the pedicle valve. Sarycheva says that her genus is similar to *Ovatia*, but separates the two by reason of *Ovatia's* smaller size, trifid cardinal process (the description of Muir-Wood & Cooper 1960) and its short lateral ridges. Such differences could be attributed to the smaller size and less developed morphology of *Ovatia*, provided that the cardinal process is more similar than was envisaged by Sarycheva. If the genera are distinctive it is likely that *Balakhonia* may usefully receive some of the British Lower Carboniferous species, but until specimens or better illustrations are available of the Russian genus, the Fermanagh material is tentatively assigned to *Ovatia*.

Family **PRODUCTELLIDAE** Schuchert & Le Vene 1929

Chonopectinid sp.

(Pl. 19, figs. 11–16)

Measurements (in mm.)

	length	width
Complete brachial valve (BB.52948)	7·1	12·4
Incomplete brachial valve (BB.52949)	7·6	—

This material consists of about a dozen complete or incomplete brachial valves of doubtful systematic position and with no known matching pedicle valves. These brachial valves are subrectangular in outline, a little over one-half as long as wide, with a straight hinge-line commonly forming the widest part of the valve ; they are flat to gently concave in profile, but irregular, and the ornamentation of concentric sublamellose rugae is irregular and usually distorted as if by close contact with some

foreign object, such as a fenestellid colony. The hypercline interarea is short and extends almost the full hinge width ; the notothyrium is filled by the base of the cardinal process and narrow dorsal ends of the sockets. The cardinal process is bilobed, quadrifid and perpendicular to the commissural plane, its myophores are posteriorly directed and the two lobes are only narrowly separated. The cardinal process is supported by a low short median septum extending about one-quarter of the valve length, and by short socket ridges that tend to recurve to the interarea. The interior is otherwise devoid of markings, save for a representation of the external ornamentation.

The short interarea and presence of sockets indicates that the shells possessed teeth, and the pedicle valve was probably convex to allow for the body cavity. The Fermanagh valves match a single brachial valve (B.53687) collected from Thorpe Cloud, Derbyshire, which is amongst specimens of *Chonetipustula carringtoniana*. However, it is quite distinct from that species and could only doubtfully be assigned to *Chonetipustula* because of its thickened shell and cardinal process which is more reminiscent of the strophalosids. *Chonetipustula* has been placed in the subfamily Chonopectinae by Muir-Wood & Cooper (1960). At the same time these authors erected a new genus, *Quadratia*, with *Productus hirsutiformis* Walcott as type species. This genus has similarities to the present material, but apparently has a less well defined rugation and is internally tuberculate.

Thus, although the cardinal process is strophalosiid in nature, the general outline and characters as yet known are suggestive of the species belonging to the Chonopectinae. However, the specimens cannot be assigned to any of the genera yet described.

The description of this material has been given last because of its doubtful systematic position, but the author agrees with Muir-Wood in considering the productellinids to display primitive features within the Productacea.

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PLATE 1

Heteralosia slocomi R. E. King

FIGS. 1–4. Two specimens, collected from the type locality of the Wayland formation, Texas, viewed ventrally and dorsally. U.S. Nat. Mus. ×1·6.

" ***Strophalosia*** cf. ***gerardi*** " W. King

FIG. 5. Ventral view of a Tasmanian shell to which are attached several juvenile shells. B.M. (N.H.) 98216. ×1·6.

FIG. 6. Dorsal view of same shell. ×1·6.

Strophalosia gerardi W. King

FIG. 7. Incomplete brachial valve interior from the ?Permian of the Himalayas. ×1·5. Galway University College.

FIG. 8, 9. Ventral and dorsal views of the Holotype from the Himalayas. Galway University College. FC, D. 267. ×1·5.

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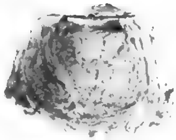

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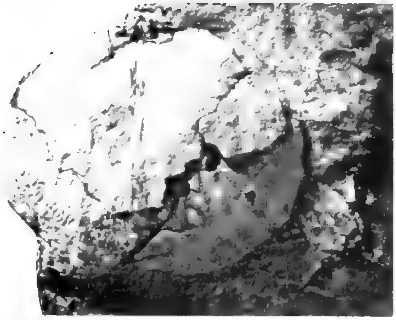

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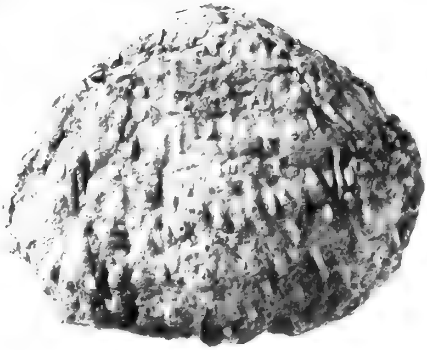

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PLATE 2

Dasyalosia panicula sp. n.

FIGS. 1–4. Shell exterior viewed dorsally, laterally, posteriorly and ventrally. BB.52790. ×2·5.

FIGS. 5, 6. Pedicle valve exterior and interior. BB.52793. ×4·5.

FIG. 7. Pedicle valve interior. BB.52791. ×3·3.

FIG. 8. Brachial valve interior. BB.52795. ×5.

FIGS. 9, 10. Incomplete pedicle valve exterior and interior. BB.52792. ×4·3.

FIGS. 11, 12. Brachial valve exterior and interior. BB.52794. ×4·3.

FIG. 13. Incomplete pedicle valve exterior. BB.52799. ×2·5.

FIGS. 14, 15. Shell exterior viewed dorsally and ventrally. BB.52796. ×6.

FIGS. 16, 17. Pedicle valve exterior, ventral and lateral views. BB.52800. ×3·1.

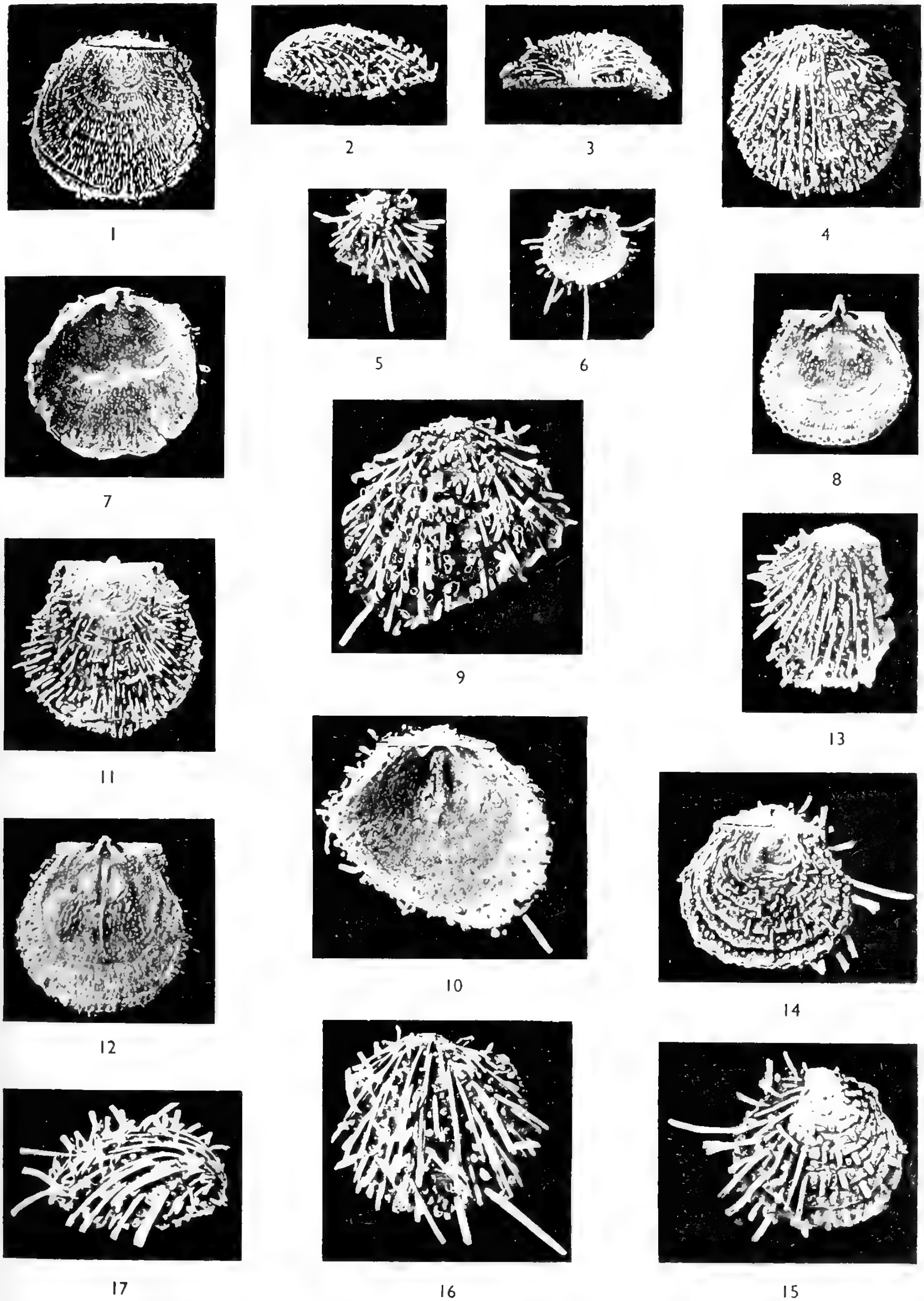
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PLATE 3

Dasyalosia panicula sp. n.

FIG. 1. Pedicle valve, viewed dorsally, attached to bryozoan. BB.52797. ×4·5.

FIGS. 2, 3. Pedicle valve, viewed externally and internally, attached to bryozoan. BB.52920. ×4·5.

FIGS. 4, 5. Pedicle valve, viewed internally and externally, attached to bryozoan. BB.52798. ×4·7.

Dasyalosia lamnula sp. n.

FIG. 6. Brachial valve interior. BB.52807. ×4·8.

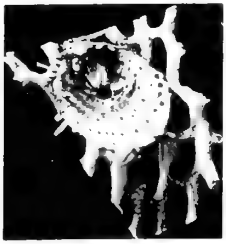
FIG. 7. Pedicle valve exterior. BB.52804. ×3·1.

FIGS. 8–10. Incomplete brachial valve viewed posteriorly, internally and externally. BB.52809. ×5.

FIGS. 11–14. Shell exterior viewed posteriorly, laterally, dorsally and ventrally. BB.52801. ×3·5.

FIGS. 15, 16. Pedicle valve exterior and interior. BB.52803. ×3·5.

FIGS. 17, 18. Incomplete pedicle valve interior and exterior. BB.52802. ×2·5.



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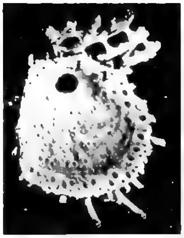

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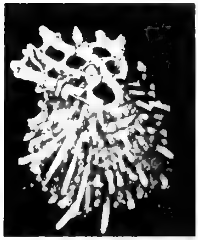

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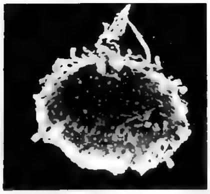

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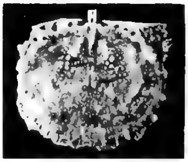

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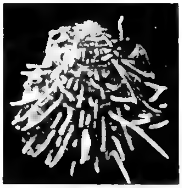

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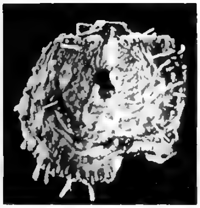

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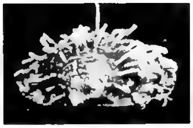

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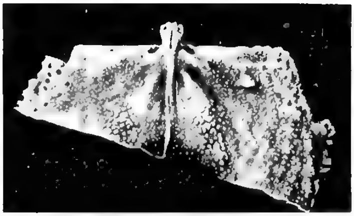

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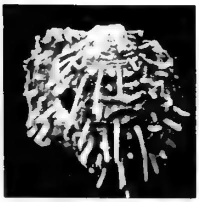

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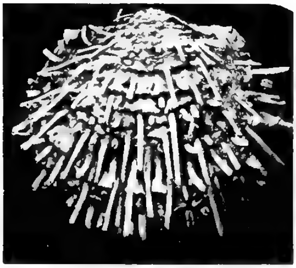

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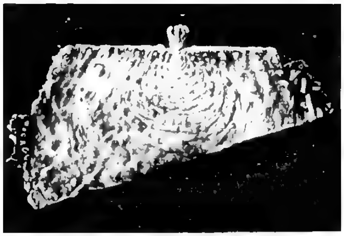

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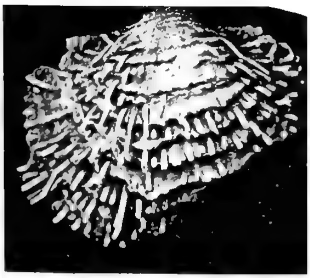

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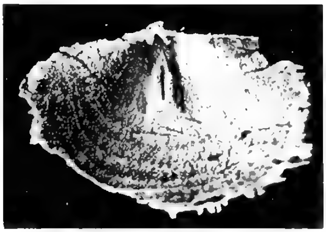

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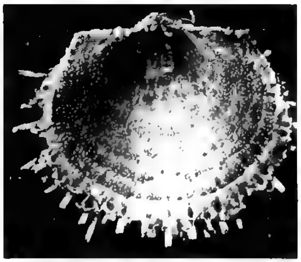

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PLATE 4

Dasyalosia lamnula sp. n.

FIGS. 1, 2. Incomplete brachial valve exterior and interior. BB.52806. ×2·5.
FIG. 3. Pedicle valve exterior. BB.52812. ×9·5.
FIG. 4. Pedicle valve exterior. BB.52811. ×7.
FIG. 5. Incomplete pedicle valve interior. BB.52805. ×3·1.
FIG. 6. Brachial valve interior. BB.52808. ×4·6.
FIGS. 7, 8. Incomplete brachial valve viewed posteriorly and internally. BB.52810. ×5·3.

Heteralosia cf. ***fortispinosa*** (Hinchey & Ray)

FIGS. 9, 10. Brachial valve exterior and interior. BB.52820. ×5.
FIGS. 11–13. Brachial valve viewed internally, externally and postero-dorsally. BB.52819. ×5.
FIGS. 14, 15. Pedicle valve viewed externally and internally attached to shell debris. BB. 52825. ×4·8.
FIGS. 16–19. Shell exterior viewed laterally, ventrally, posteriorly and dorsally. BB.52813. ×4·4.

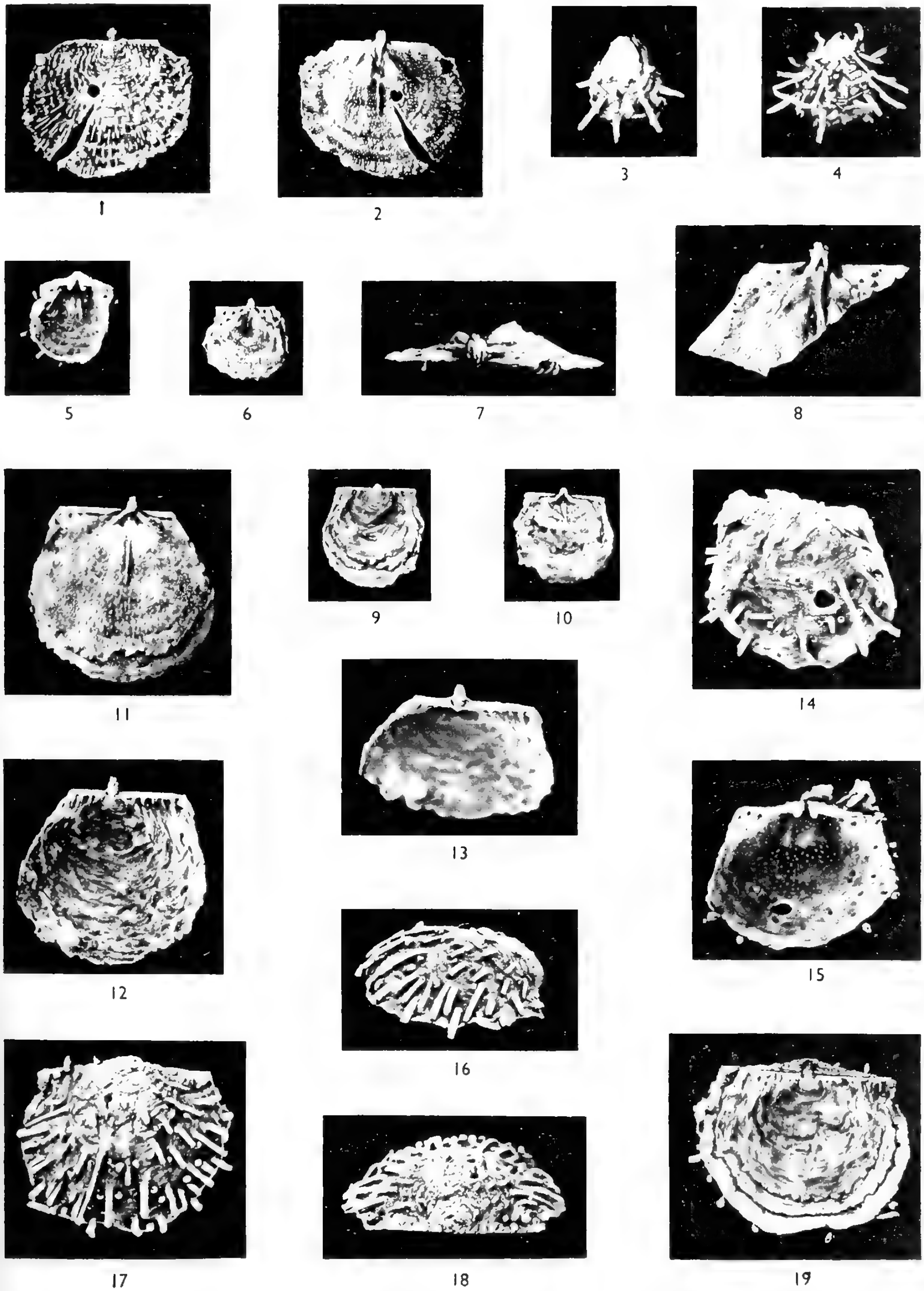
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PLATE 5

Heteralosia cf. ***fortispinosa*** (Hinchey & Ray)

FIG. 1. Incomplete pedicle valve interior. BB.52824. ×4·5.

FIGS. 2, 3. Incomplete brachial valve viewed internally and postero-ventrally. BB.52818. ×3·3.

FIG. 4. Pedicle valve attached to shell debris. BB.52826. ×4·5.

FIG. 5. Incomplete brachial valve interior. BB.52817. ×3·6.

FIG. 6. Pedicle valve exterior. BB.52822. ×5.

FIG. 7. Pedicle valve exterior. BB.52823. ×5.

FIG. 8. Pedicle valve exterior. BB.52821. ×5.

FIGS. 9–12. Pedicle valve exterior, interior, lateral exterior and interior viewed antero-dorsally. BB.52814. ×1·6.

FIG. 13. Fragment of pedicle valve exterior. BB.52816. ×3·6.

FIGS. 14, 15. Pedicle valve interior and exterior. BB.52816. ×4·5.

Acanthoplecta mesoloba (Phillips)

FIGS. 16, 17. Incomplete brachial valve exterior and interior. BB.52829. ×2·4.

FIGS. 18, 19. Incomplete shell exterior viewed ventrally and dorsally. BB.52828. ×2·2

FIGS. 20, 21. Incomplete brachial valve viewed internally (×2) and postero-ventrally (×3). BB.52830.

FIG. 22. Incomplete pedicle valve exterior. BB.52827. ×1·6.

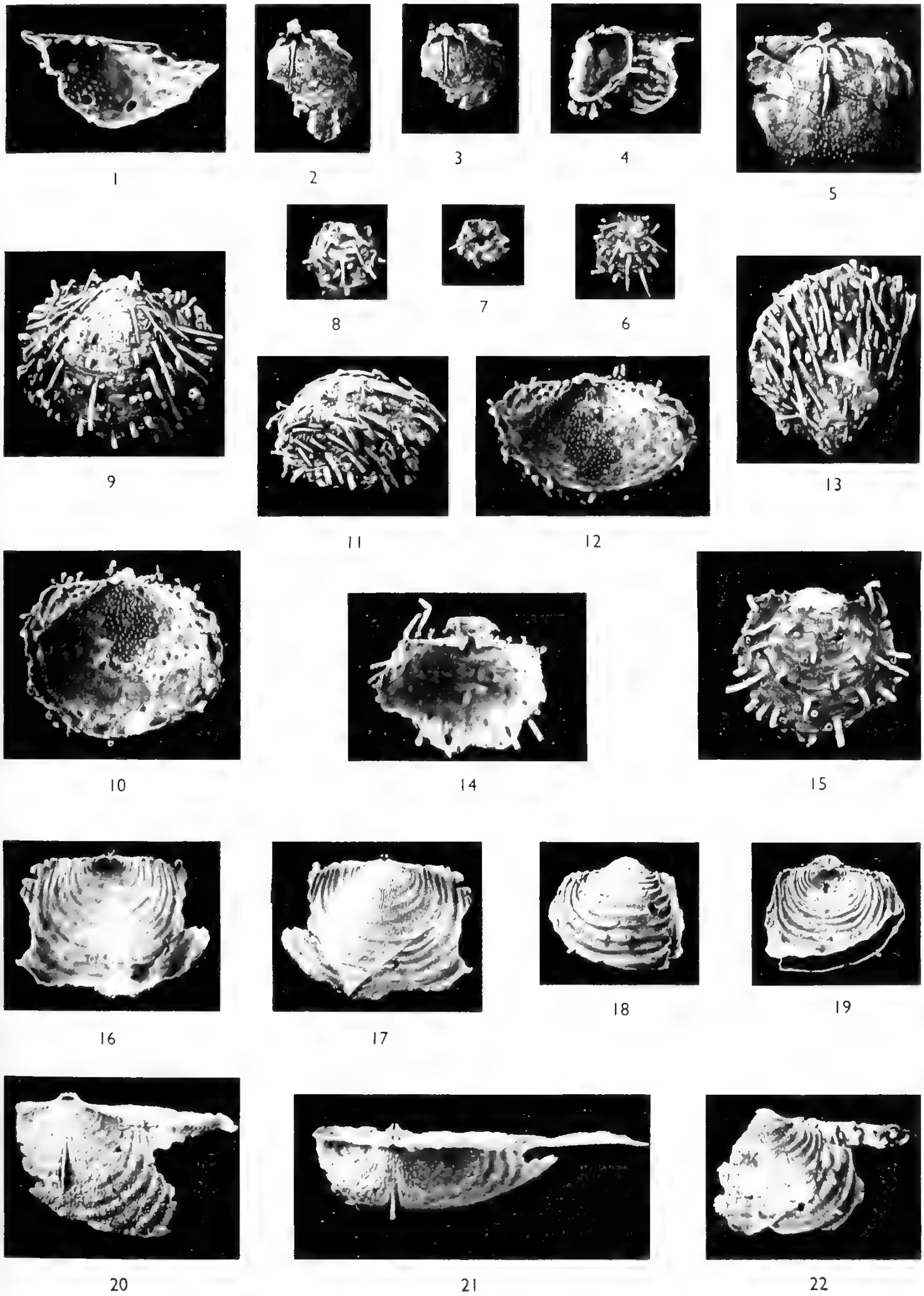
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PLATE 6

Acanthoplecta mesoloba (Phillips)

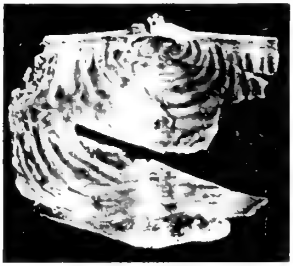
FIGS. 1–5. Incomplete brachial valve viewed dorsally, postero-dorsally ($\times$ 1·9), laterally, ventrally and antero-ventrally. BB.52831. $\times$ 1·3.

Plicatifera plicatilis (J. de C. Sowerby)

FIGS. 6–10. Pedicle valve viewed laterally, antero-ventrally, dorsally, dorso-laterally and posteriorly. BB.52832. $\times$ 1·7.

FIGS. 11, 12. Brachial valve posteriorly ($\times$ 4·7) and internally ($\times$ 3). BB.52836.

FIGS. 13–15. Brachial valve viewed externally, antero-ventrally and ventrally. BB.52833. $\times$ 1·5.



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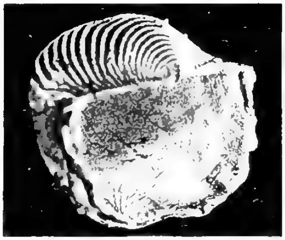

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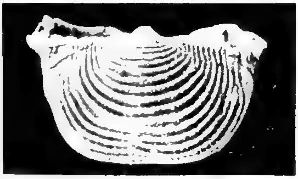

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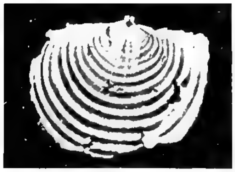

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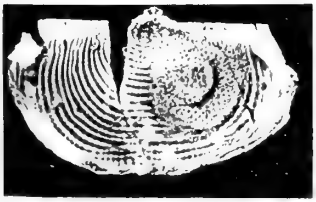

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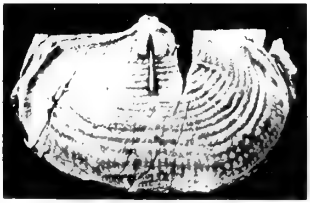

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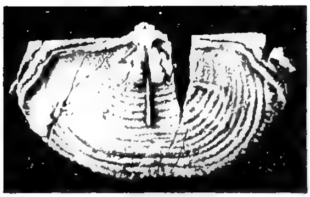

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PLATE 7

Plicatifera plicatilis (J. de C. Sowerby)

FIGS. 1–3. Pedicle valve, attached to bryozoan, viewed dorsally, posteriorly and ventrally. BB.52843. ×10·1.

FIGS. 4, 5. Incomplete pedicle valve interior and exterior. BB.52840. ×10·1.

FIG. 6. Fragment of brachial valve interior. BB.52839. ×10·1.

FIGS. 7, 8. Pedicle valve exterior and interior. BB.52844. ×7·4.

FIG. 9. Incomplete pedicle valve interior. BB.52838. ×1·9.

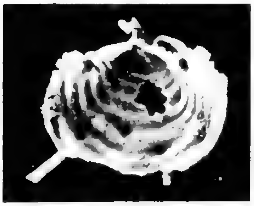
FIG. 10. Pedicle valve exterior. BB.52841. ×12.

FIGS. 11, 12. Incomplete pedicle valve exterior and interior. BB.52842. ×10·1.

FIGS. 13–15. Incomplete brachial valve viewed ventrally, dorsally and posteriorly. BB.52835. ×1·7.

FIGS. 16, 17. Incomplete shell interior viewed anteriorly and antero-laterally. BB.52837. ×1·7.

FIG. 18. Incomplete pedicle valve interior. BB.52834. ×1·9.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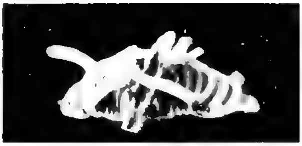
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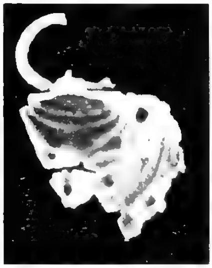
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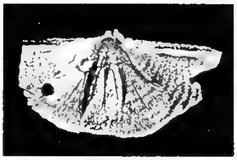
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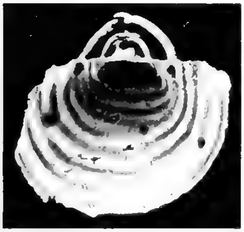
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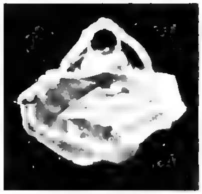
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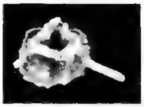
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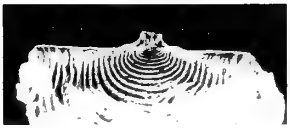
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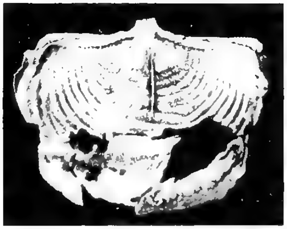
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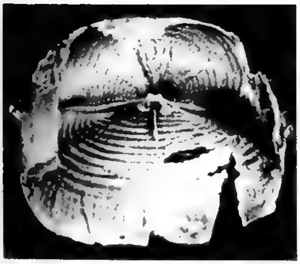
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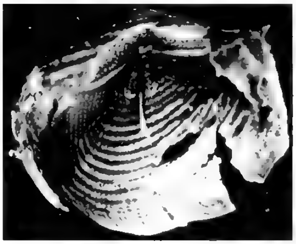
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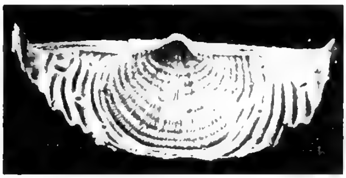
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PLATE 8

Productina margaritacea (Phillips)

FIGS. 1–4. Shell exterior viewed laterally, posteriorly, dorsally and ventrally. BB.52904. ×1·4.

FIG. 5. Incomplete pedicle valve interior. BB.52913. ×5.

FIGS. 6, 7. Incomplete shell viewed ventrally and dorsally. BB.52905. ×1·4.

FIGS. 8, 9. Brachial valve exterior and interior. BB.52909. ×1·5.

FIGS. 10–12. Incomplete pedicle valve viewed ventrally, dorsally and antero-dorsally. BB.52907. ×2·3.

FIG. 13. Pedicle valve interior. BB.52906. ×3·7.

FIGS. 14, 15. Incomplete pedicle valve viewed posteriorly and ventrally. BB.52908. ×3·7.

FIG. 16. Incomplete pedicle valve interior. BB.52916. ×6·5.

FIGS. 17–19. Pedicle valve viewed dorsally (×5·5), antero-dorsally and postero-ventrally. BB.52912. ×6.

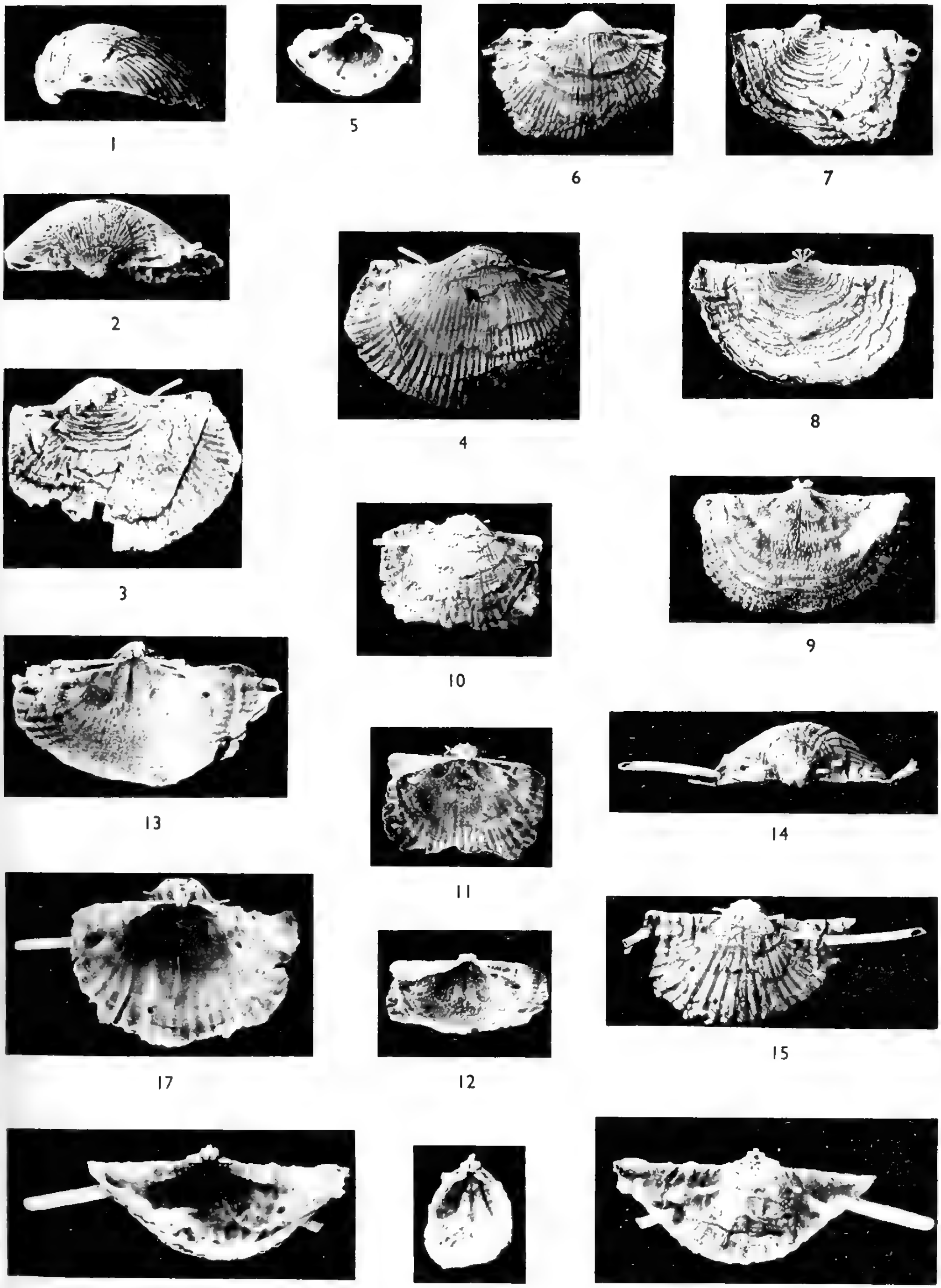
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PLATE 9

Overtonia fimbriata (J. de C. Sowerby)

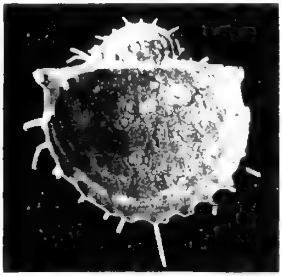
FIGS. 1–4. Pedicle valve viewed dorsally, anteriorly, antero-dorsally and ventrally. BB. 52846. ×1·9.

FIG. 5. Fragment of pedicle valve interior. BB. 52852. ×3.

FIGS. 6–8. Brachial valve viewed dorsally, postero-ventrally and ventrally. BB. 52847. ×2.

FIG. 9. Incomplete brachial valve interior. BB. 52848. ×2·5.

FIGS. 10–13. Shell exterior viewed postero-ventrally, ventrally, laterally and dorsally. BB. 52845. ×2·2.



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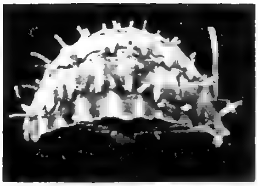

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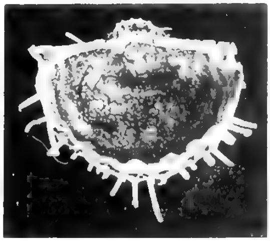

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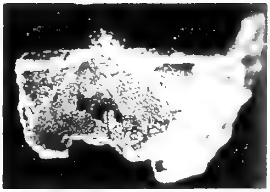

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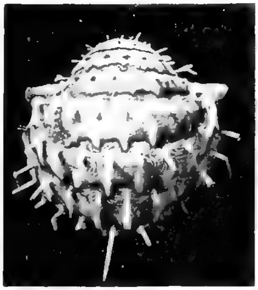

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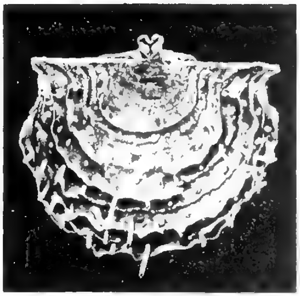

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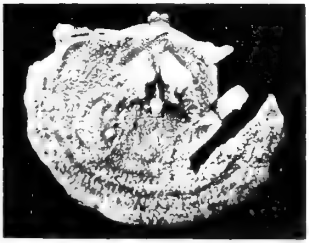

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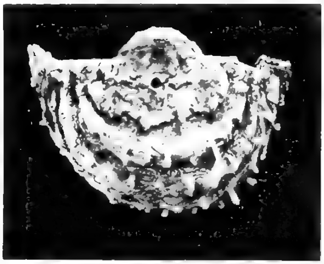

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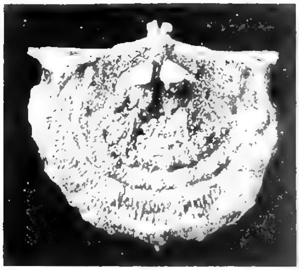

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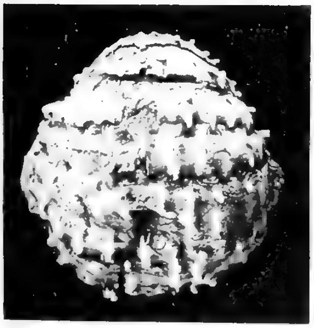

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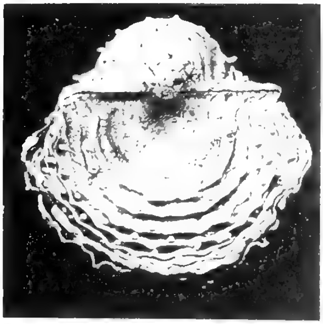

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PLATE 10

Overtonia fimbriata (J. de C. Sowerby)

FIGS. 1–3. Brachial valve viewed dorsally, postero-ventrally and ventrally. BB.52849. ×3.

FIG. 4. Pedicle valve exterior. BB.52851. ×3.

FIGS. 5–7. Shell exterior, posteriorly, dorsally and ventrally. BB.52850. ×3.

Avonia (Quasiavonia) aculeata (J. Sowerby)

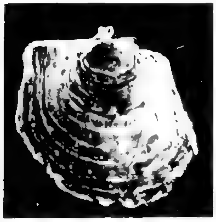
FIGS. 8–11. Shell exterior viewed ventrally, posteriorly, laterally and dorsally. BB.52853. ×1·5.

FIGS. 12, 13. Incomplete brachial valve postero-ventrally and postero-dorsally. BB.52856. ×3·7.

FIG. 14. Pedicle valve exterior. BB.52857. ×2·7.

FIGS. 15, 16. Brachial valve viewed ventrally and postero-ventrally. BB.52855. ×2.

FIG. 17. Incomplete pedicle valve interior. BB.52858. ×2.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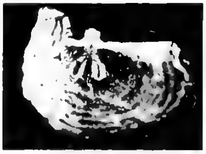
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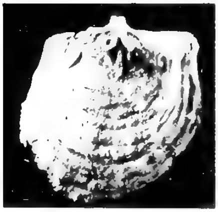
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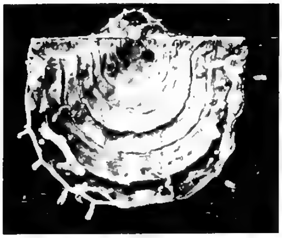
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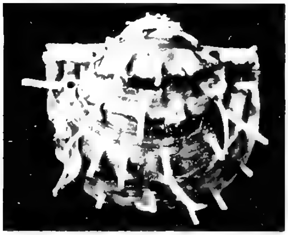
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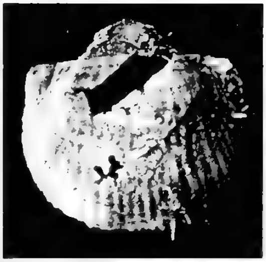
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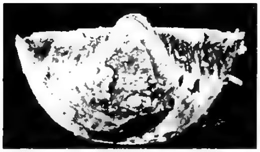
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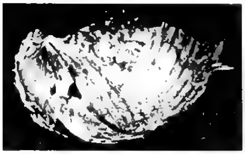
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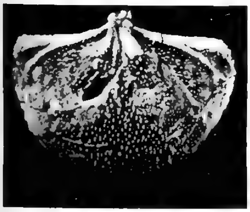
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PLATE 11

Avonia (Quasiavonia) aculeata (J. Sowerby)

FIGS. 1–4. Shell exterior viewed dorsally, posteriorly, laterally and ventrally. BB.52859. ×1·6.

FIGS. 5–7. Brachial valve viewed postero-ventrally, dorsally and ventrally. B.52864. ×6.

FIG. 8. Incomplete pedicle valve interior. BB.52860. ×1·7.

FIGS. 9–11. Pedicle valve viewed ventrally dorsally and antero-dorsally. BB.52866. ×7·8.

FIGS. 12–14. Shell exterior viewed ventrally, posteriorly and dorsally. BB.52863. ×2.

FIGS. 15–17. Incomplete brachial valve viewed posteriorly, ventrally and dorsally. BB. 52862. ×2·4.

FIGS. 18, 19. Brachial valve, exterior and interior. BB.52865. ×6.

FIG. 20. Incomplete pedicle valve interior. BB.52862. ×2·4.

FId. 21. Incomplete shell viewed postero-laterally. BB.52862. ×2·4.

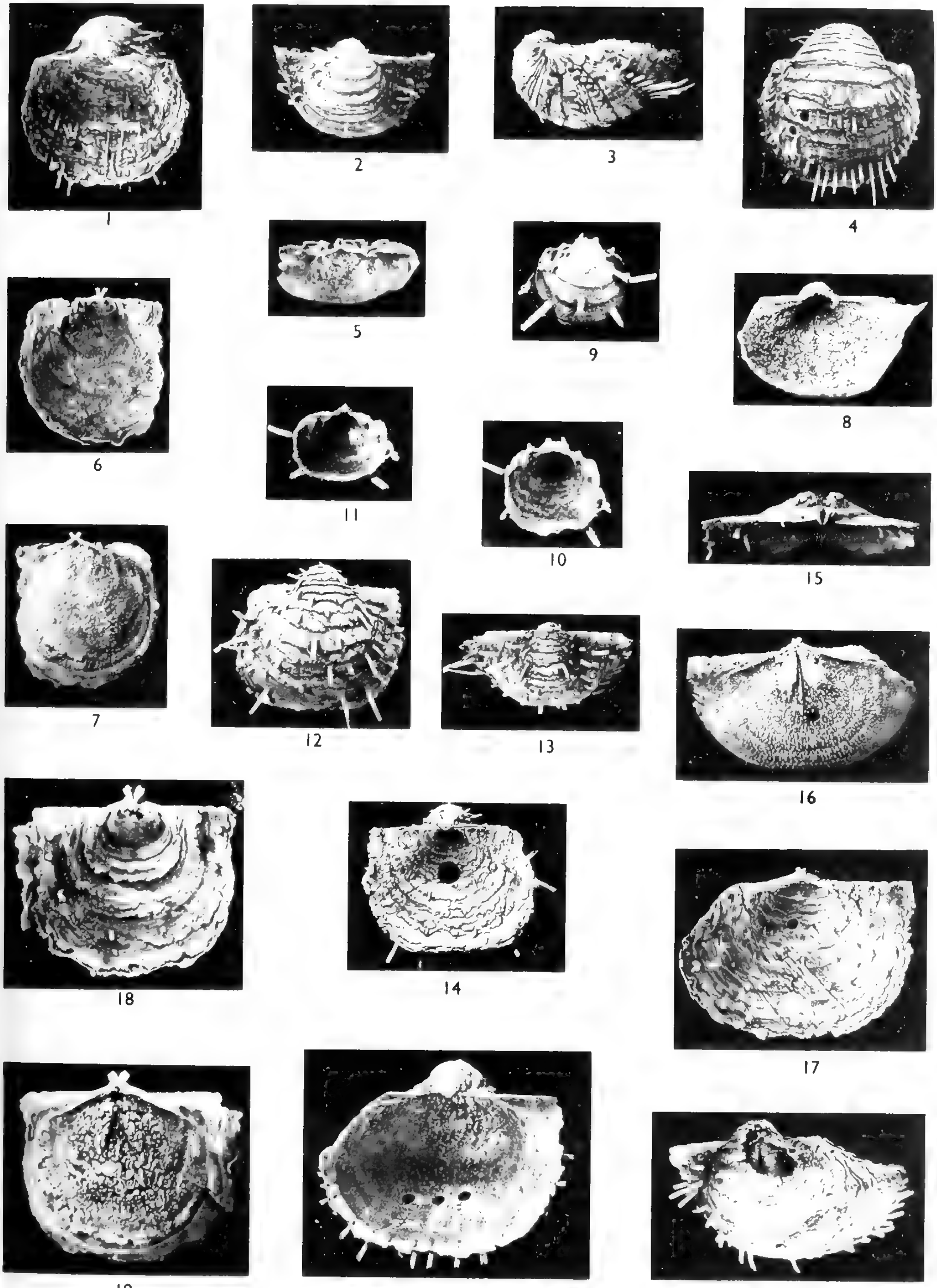
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PLATE 12

Krotovia spinulosa (J. Sowerby)

FIGS. 1–4. Shell exterior viewed posteriorly, ventrally, laterally and dorsally. BB.52867. ×2·3.

FIGS. 5, 6. Brachial valve exterior and interior. BB.52884. ×8·2.

FIGS. 7, 8. Pedicle valve interior and exterior. BB.52870. ×4.

FIGS. 9, 10. Brachial valve exterior and interior. BB.52875. ×3·6.

FIGS. 11–13. Incomplete brachial valve viewed posteriorly, dorsally and ventrally. BB. 52873. ×3·6.

FIGS. 14, 15. Brachial valve exterior (×3·3) and interior (×4·5). BB.52871.

FIGS. 16–18. Incomplete brachial valve viewed postero-dorsally, dorsally and ventrally. BB.52872. ×4·5.

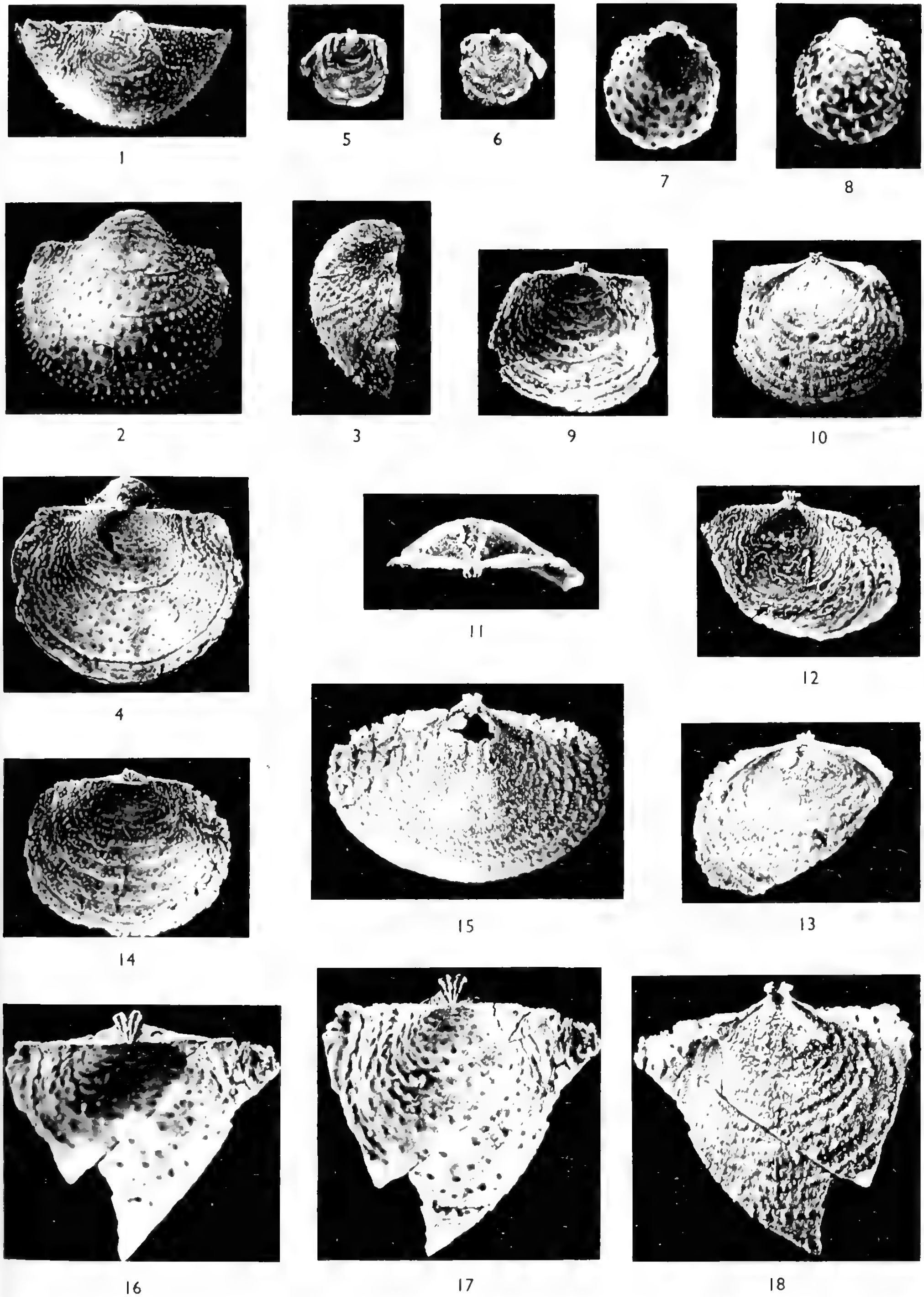
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PLATE 13

Krotovia spinulosa (J. Sowerby)

FIGS. 1, 2. Shell exterior viewed ventrally and dorsally. BB.52868. ×4.

FIG. 3. Incomplete pedicle valve exterior. BB.52869. ×4.

FIGS. 4–6. Shell exterior viewed posteriorly, ventrally and dorsally. Cunningham Baidland. BB.52876. ×2.

FIG. 7. Pedicle valve exterior. Cunningham Baidland. BB.52877. ×2·3.

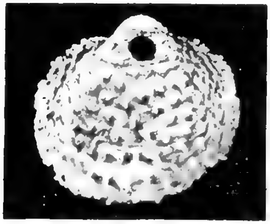
Krotovia lamellosa sp. n.

FIGS. 8–12. Shell exterior viewed dorsally, ventrally, laterally, anteriorly and posteriorly. BB.52878. ×3·2.

FIG. 13. Incomplete pedicle valve exterior. BB.52881. ×4·4.

FIGS. 14, 15. Incomplete brachial valve interior and exterior. BB.52884. ×3.

FIG. 16. Brachial valve interior. BB.52885. ×6.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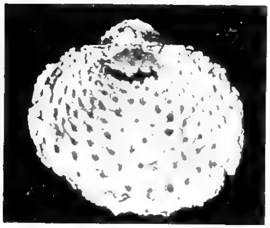
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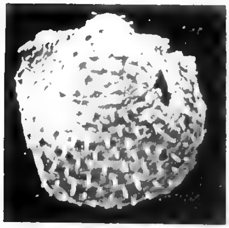
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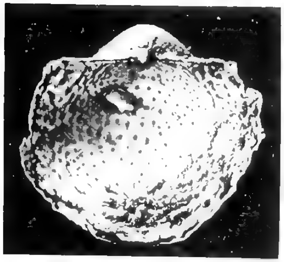
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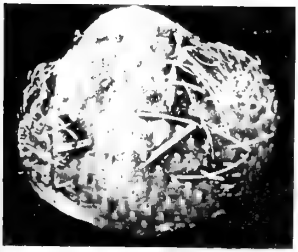
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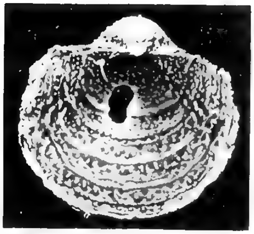
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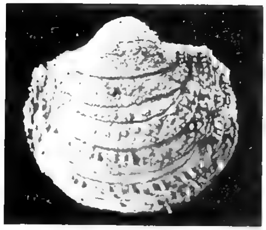
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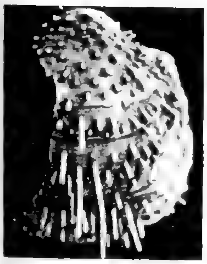
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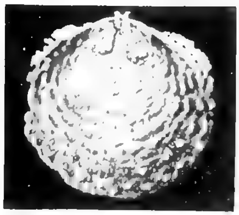
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PLATE 14

Krotovia lamellosa sp. n.

FIGS. 1, 2. Pedicle valve exterior and interior. BB.52888. ×10.

FIGS. 3, 4. Pedicle valve interior and exterior. BB.52889. ×10.

FIG. 5. Incomplete pedicle valve interior. BB.52882. ×5.

FIGS. 6, 7. Incomplete brachial valve exterior and interior. BB.52886. ×6.

FIGS. 8–11. Brachial valve viewed postero-dorsally (×3·6), ventrally, posteriorly and dorsally. BB.52883. ×3.

FIGS. 12, 13. Incomplete brachial valve interior and exterior. BB.52887. ×8.

FIGS. 14, 15. Incomplete pedicle valve viewed laterally and ventrally. BB.52880. ×4·4.

FIGS. 16–19. Pedicle valve viewed antero-dorsally, dorsally, posteriorly and ventrally. BB.52879. ×3.

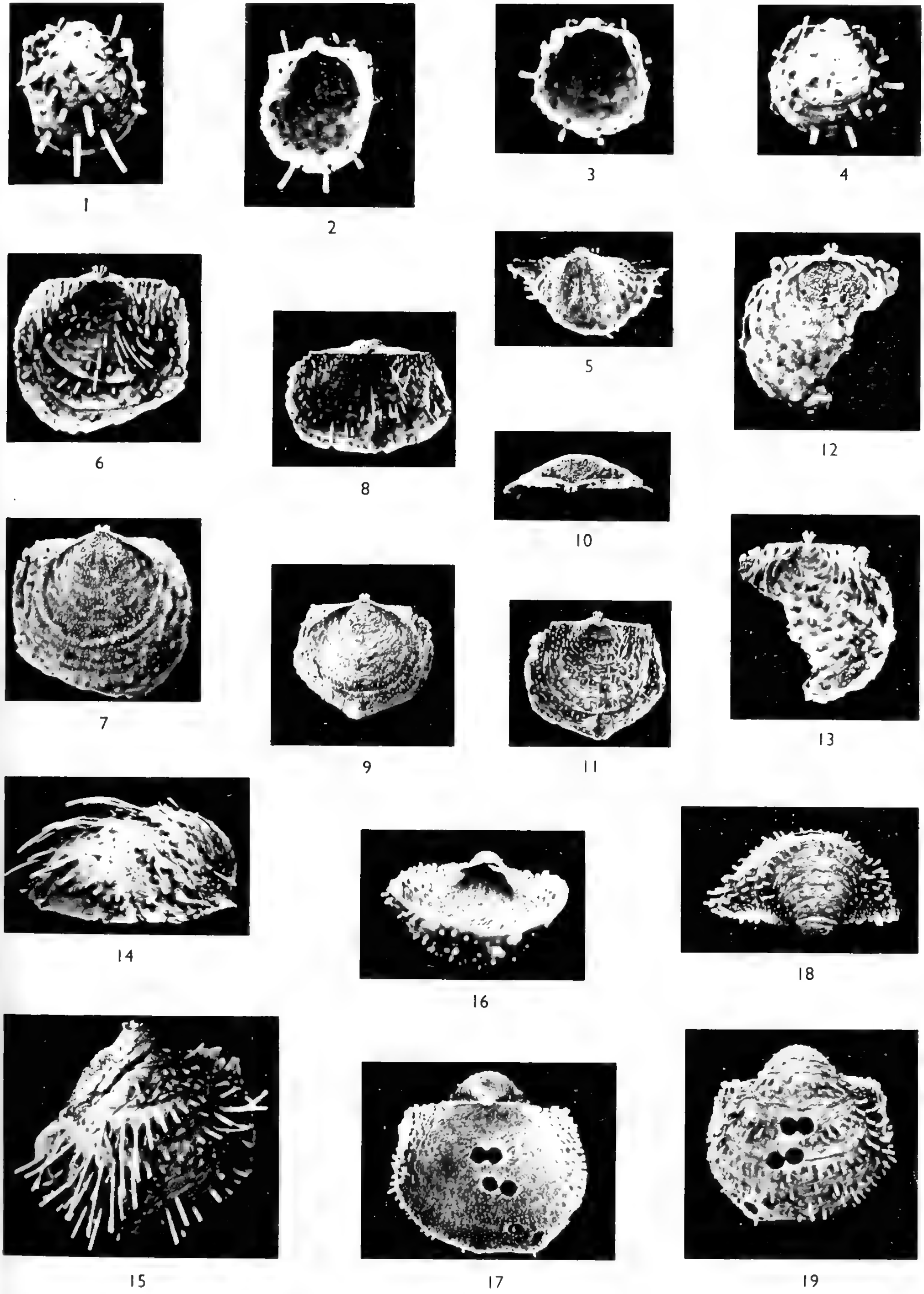

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PLATE 15

Productina margaritacea (Phillips)

FIGS. 1–3. Incomplete pedicle valve viewed dorsally, ventrally and antero-dorsally. BB. 52914. ×5.

FIG. 4. Brachial valve interior. BB.52910. ×4·8.

FIGS. 5, 6. Incomplete pedicle valve exterior and interior. BB.52915. ×6·5.

FIGS. 7, 8. Incomplete brachial valve exterior and interior. BB.52911. ×6·5.

Eomarginifera (Eomarginiferina) trispina subgen. et sp. n.

FIG. 9. Incomplete pedicle valve exterior. BB.52901. ×7·2.

FIGS. 10–13. Brachial valve viewed postero-dorsally and postero-ventrally (×4) and antero-ventrally and ventrally (×2·7). BB.52895.

FIGS. 14–17. Incomplete shell viewed ventrally, dorsally, posteriorly and laterally. BB. 52903. ×3·1.

FIGS. 18–21. Shell viewed laterally, posteriorly, ventrally (×2·7) and antero-dorsally (×4). BB.52890.

FIG 22. Incomplete pedicle valve exterior. BB.52898. ×3.

PLATE 15

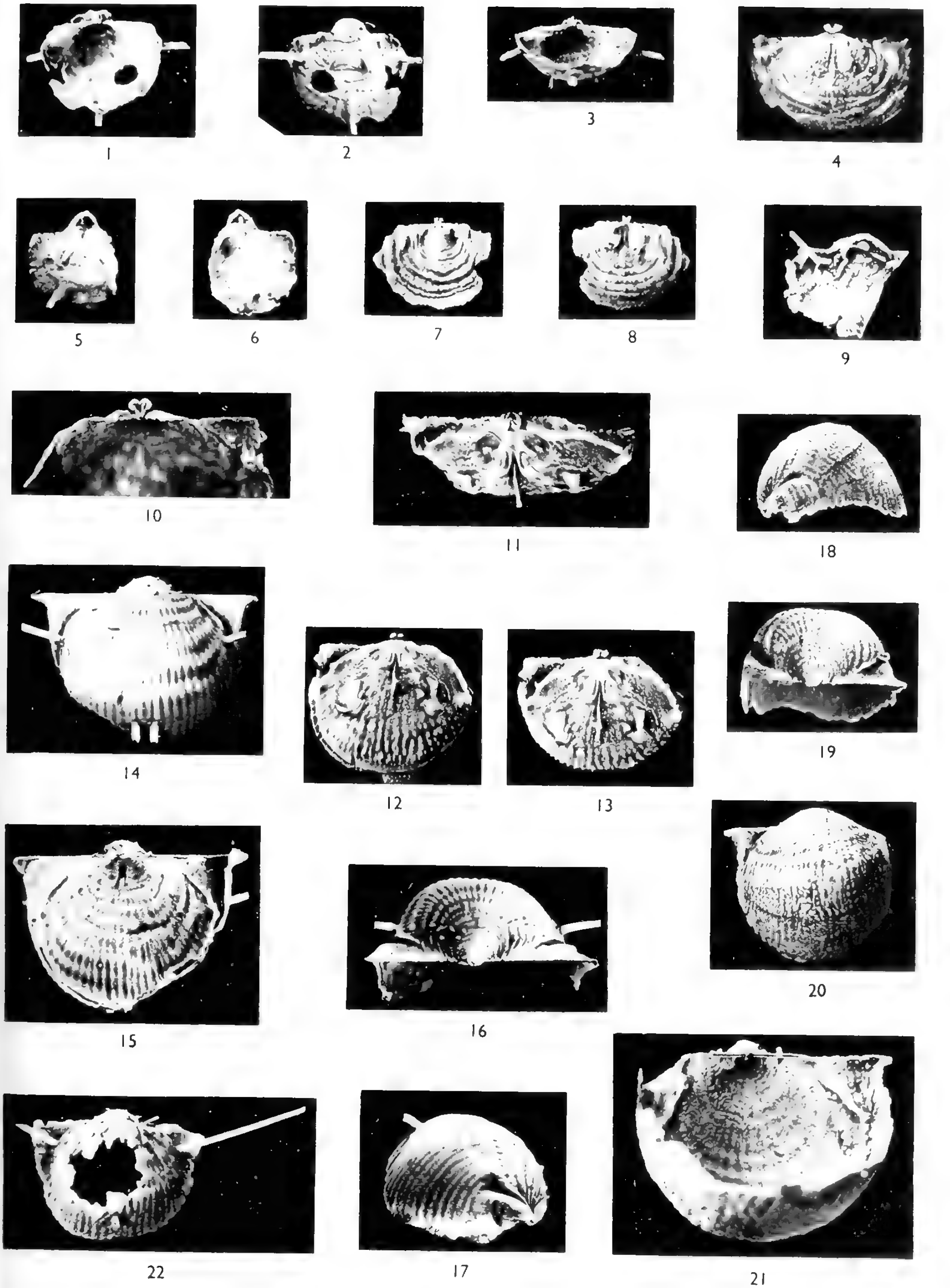

PLATE 16

Eomarginifera (Eomarginiferina) trispina subgen. et sp. n.

FIGS. 1–3. Pedicle valve viewed ventrally, dorsally and antero-dorsally. BB.52900. ×7.

FIG. 4. Incomplete pedicle valve exterior. BB.52902. ×7.

FIGS. 5–7. Incomplete shell viewed posteriorly, dorsally and antero-ventrally. BB.52899. ×3.

FIGS. 8, 9. Brachial valve exterior and interior. BB.52897. ×3.

FIGS. 10, 11. Brachial valve exterior and interior. BB.52896. ×3.

FIGS. 12–15. Shell viewed dorsally, laterally, anteriorly and ventrally. BB.52891. ×2·7.

FIGS. 16–20. Pedicle valve viewed laterally, posteriorly, dorsally, antero-dorsally and postero-ventrally. BB.52893. ×3.

FIGS. 21, 22. Pedicle valve interior viewed antero-dorsally and dorsally. BB.52892. ×3·7.

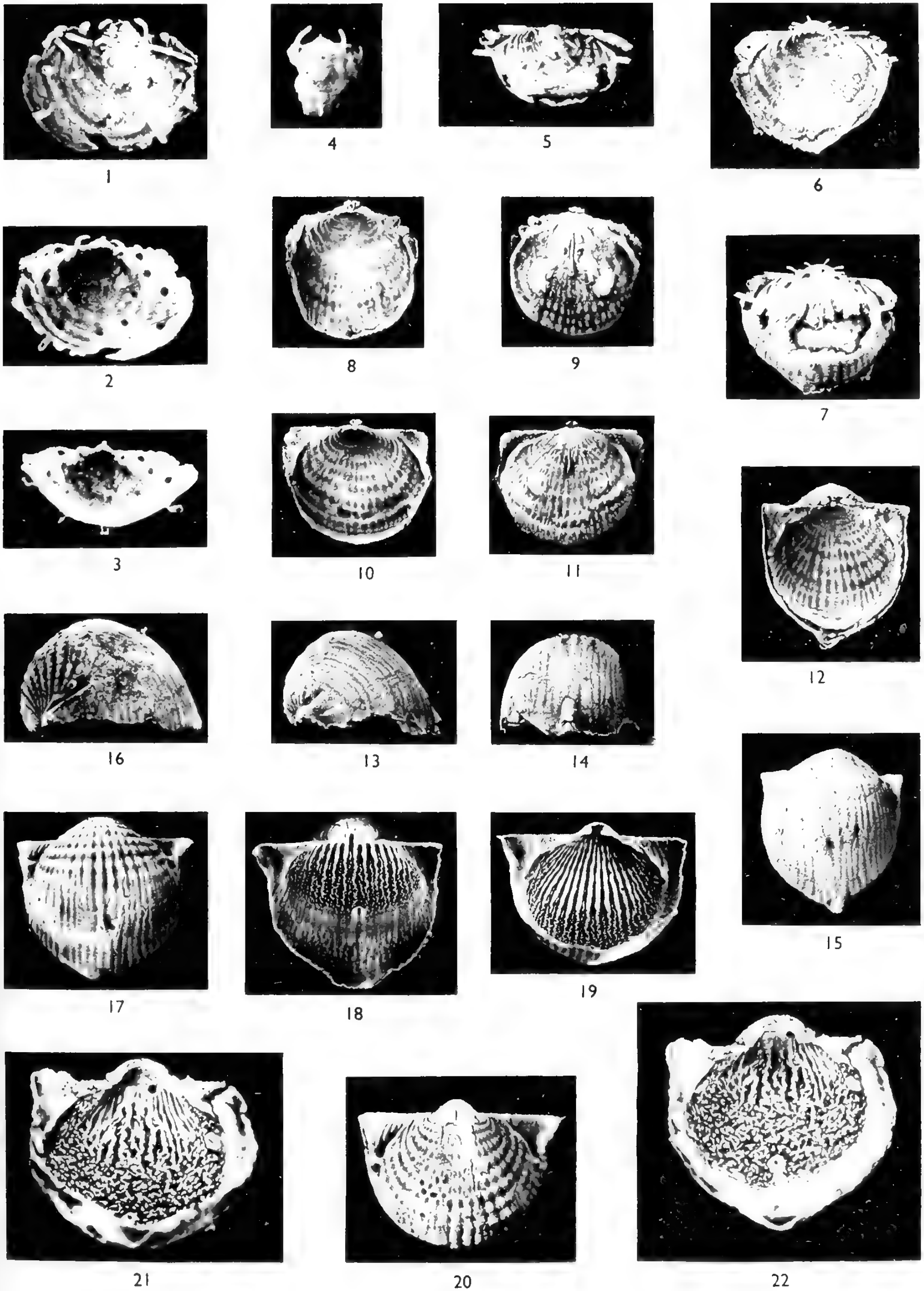

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PLATE 17

Antiquatonia sp.

FIGS. 1.–6. Pedicle valve viewed posteriorly, postero-ventrally, dorsally, laterally, antero-ventrally and antero-dorsally. BB.52934. ×0·85.

FIGS. 7–10. Incomplete brachial valve viewed ventrally, dorsally, and two posterior views. BB.52935. ×2.

Echinoconchus cf. *punctatus* (J. Sowerby)

FIGS. 11, 12. Incomplete pedicle valve interior and exterior. BB.52937. ×1·5.

FIG. 13. Incomplete brachial valve interior. BB.52939. ×1·5.

FIGS. 14, 15. Pedicle valve viewed posteriorly and ventrally. BB.52936. ×2·5.


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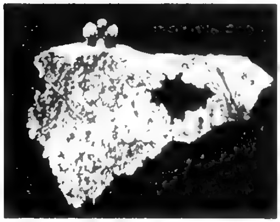
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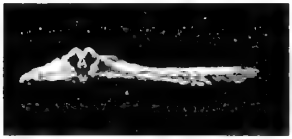
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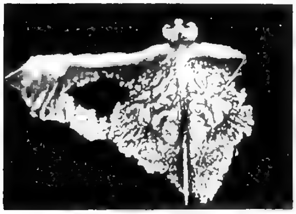
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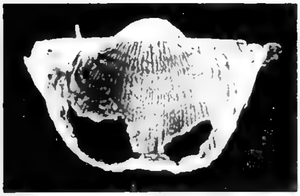
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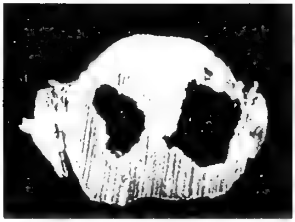
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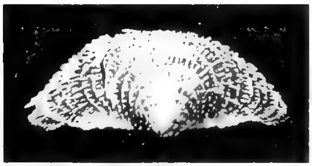
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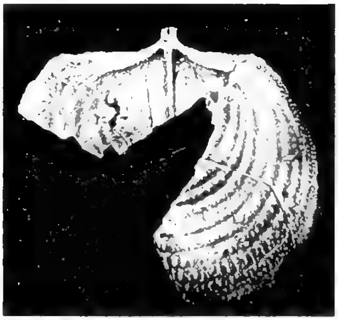
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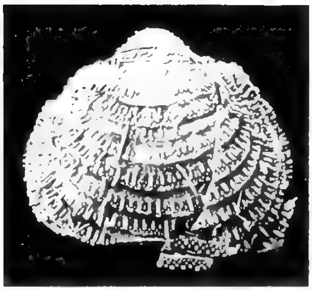
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PLATE 18

Echinoconchus cf. *punctatus* (J. Sowerby)

FIGS. 1, 2. Incomplete brachial valve viewed dorsally and postero-ventrally. BB.52939. ×1·5.

FIGS. 3, 4. Incomplete brachial valve exterior and interior. BB.52938. ×1·75.

Pustula cf. *pyxidiformis* (de Koninck)

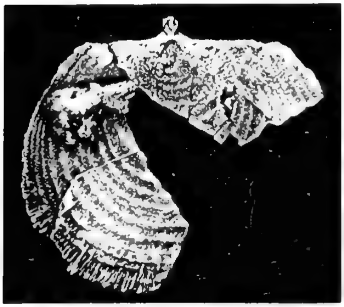
FIGS. 5–7. Incomplete pedicle valve exterior and interior. BB.52940. ×0·85.

FIGS. 8, 9. Crushed shell viewed antero-dorsally, showing the cardinal process, and dorsally, with a fragment of an orthotetinid pedicle valve. BB.52942. ×0·9.

FIGS. 10. Incomplete brachial valve viewed posteriorly. BB.52944. ×1·5.

FIGS. 11, 12. Crushed shell viewed antero-dorsally and ventrally. BB.52941. ×0·85.

FIGS. 13, 14. Incomplete brachial valve interior and exterior.



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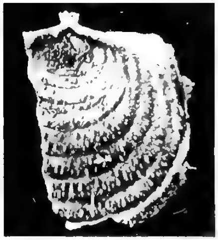

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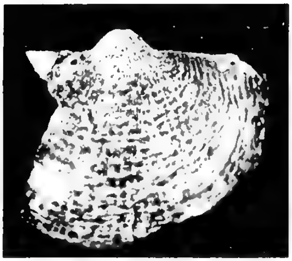

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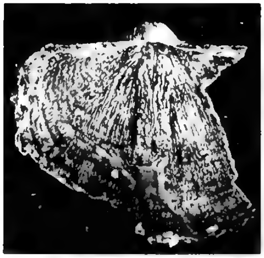

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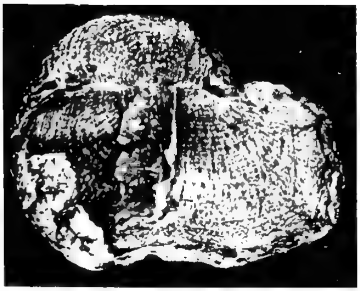

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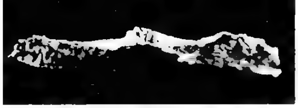

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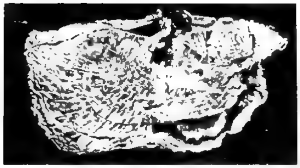

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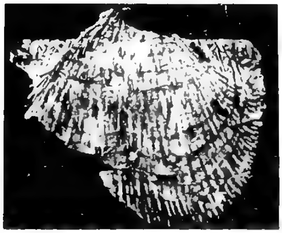

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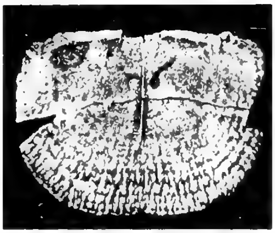

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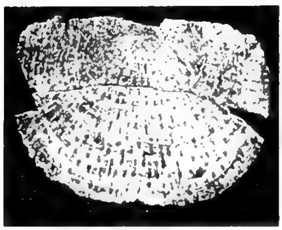

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PLATE 19

Pustula cf. ***pyxidiformis*** (de Koninck)

FIGS. 1, 2. Incomplete brachial valve interior and exterior. BB.52944. ×1·5.

Ovatia sp.

FIGS. 3, 4. Incomplete brachial valve viewed internally and posteriorly. BB.52947. ×3·7.

FIGS. 5–8. Pedicle valve viewed anteriorly and posteriorly (×5) and externally and internally (×4). BB.52945.

FIGS. 9, 10. Incomplete pedicle valve interior and exterior. BB.52946. ×2·9.

Chonopectinid sp.

FIGS. 11–13. Complete brachial valve posterior, exterior and interior. BB.52948. ×3·5.

FIGS. 14–16. Incomplete brachial valve posterior, exterior and interior. BB.52949. ×3·5.

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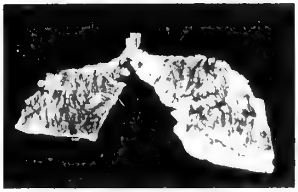

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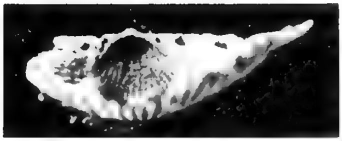

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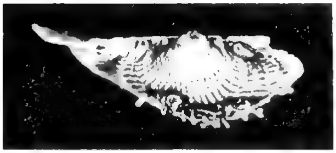

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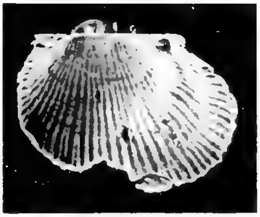

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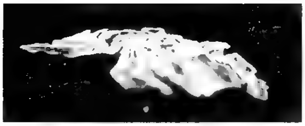

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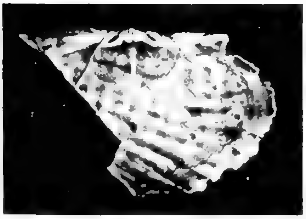

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NATURAL HISTORY

THE LOWER ORDOVICIAN STRATIGRAPHY AND TRILOBITES OF THE LANDEYRAN VALLEY AND THE NEIGHBOURING DISTRICT OF THE MONTAGNE NOIRE, SOUTH-WESTERN FRANCE

W. T. DEAN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 12 No. 6
LONDON: 1966

THE LOWER ORDOVICIAN STRATIGRAPHY AND TRILOBITES OF THE LANDEYRAN VALLEY AND THE NEIGHBOURING DISTRICT OF THE MONTAGNE NOIRE, SOUTH-WESTERN FRANCE

BY

WILLIAM THORNTON DEAN, Ph.D.

P. 245–353 ; 21 *Plates* ; 8 *Text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
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THE LOWER ORDOVICIAN STRATIGRAPHY AND TRILOBITES OF THE LANDEYRAN VALLEY AND THE NEIGHBOURING DISTRICT OF THE MONTAGNE NOIRE, SOUTH-WESTERN FRANCE

By W. T. DEAN

CONTENTS

CONTENTS—*contd.*

SYNOPSIS

The Ordovician rocks of the Montagne Noire around the Landeyran Valley are described and the following succession established, in ascending order : Schistes de Setso, Grès à Lingules, Couches du Foulon and Couches du Landeyran, the last-named being further subdivided into Couches inférieures and Couches supérieures. All these strata are assigned to the Extensus Zone of the Arenig Series. The Couches supérieures occur only in the southern half of the Landeyran Valley and are overstepped to north and south by unconformable Devonian beds. The trilobite faunas are discussed in detail and the following new species described : *Ceraurinella peregrinus*, *Ormathops borni*, *Prionocheilus matutinus*, *Colpocoryphe thorali*, *Neseuretus antetristani*, *N. arenosus*, *Platycoryphe convergens*, *Basiliella mediterranea*, *Hoekaspis? quadrata*. *Symphysurus sabulosus*, *Selenopeltis binodosus*, *Otarion insolitum* and *Apatokephalus incisus*. The relationships of the faunas with others in the Mediterranean Province and western China are discussed.

SOMMAIRE FRANÇAISE

Les roches ordoviciennes de la Montagne Noire dans la région de la vallée du Landeyran, au sud de St. Nazaire de Ladarez, sont décrites. La succession suivante est établie, en ordre ascendante : Schistes de Setso, Grès à Lingules, Couches du Foulon (après Le Foulon, une vieille maison au bord de l'Orb, au nord-est de Lugné), Couches du Landeyran inférieures et Couches du Landeyran supérieures. Toutes les couches appartiennent à l'Arenig inférieur, c'est à dire la zone de *Didymograptus extensus*. Les couches ordoviciennes sont pliées au-dessous des roches dévoniennes. Au bout nord de la vallée du Landeyran, et près du Foulon, les calcaires dolomitiques du Dévonien (le "Mur quartzeux" soi-disant) reposent avec grande discordance sur les schistes des Couches du Landeyran inférieures. Les Couches du Landeyran

supérieures ne sont que trouvées sous le Devonien dans la moitié du sud de la vallée du Landeyran, mais leur faune est connue à Boutoury, près de Cabrières, 25 km. au nord-est. La faune des Couches du Landeyran inférieures paraît plus étendue au loin, et est connue pas seulement à Boutoury mais aussi, probablement, à l'Afrique du nord. Les relations des faunes avec les autres dans la région Mediterranée sont discutées. Les trilobites sont décrits en détail et renferment les nouvelles éspèces suivantes: *Ceraurinella peregrinus. Ormathops borni, Prionocheilus matutinus, Colpocoryphe thorali, Neseuretus antetristani, N. arenosus, Platycoryphe convergens, Basiliella mediterranea, Hoekaspis? quadrata, Symphysurus sabulosus, Selenopeltis binodosus, Otarion insolitum* et *Apatokephalus incisus.*

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE south-westerly extension of the Massif Central into the départements of Hérault and Aude (part of the province of Languedoc) contains a number of mountainous districts, of which the best known to geologists is the Montagne Noire. This name is often used in a broad sense to include an area extending east-north-east from a point just north of Carcassonne towards Bédarieux and Clermont-l'Hérault. The region is separated from the Mediterranean by a coastal plain, some 30 kilometres wide, formed essentially of Mesozoic and Tertiary sediments. The Montagne Noire consists primarily of Pre-Cambrian and Palaeozoic rocks, the axial portion comprising a core of Pre-Cambrian rocks, around which are arranged successive layers of Palaeozoic strata, the whole having undergone extensive folding. Those of the southern slopes, in particular the Cambrian rocks, have long been the subject of classic research and we may, perhaps, single out the works of de Rouville and Bergeron in the last century, and of Miquel and Thoral during the present century. A long, detailed review of the considerable literature was published by Thoral (1935 : 475–483) in describing the geology of the country covered by the Bédarieux Sheet of the Service géologique de France.

In the vicinity of the town of St. Chinian, Ordovician rocks form a large curved outcrop, with maximum breadth just south of Roquebrun and narrowing to both north and south-west (see Text-fig. 1). The rock succession is in the main argillaceous, consisting of dark, concretionary mudstones and shales, together with some sandstones and, more rarely, limestones. The faunas of the sandstones are relatively sparse and poorly preserved but those of the mudstones and shales may be locally abundant, comprising especially trilobites and molluscs, with less common graptolites and brachiopods.

The Ruisseau de Landeyran (or Landayran, as it is shown on older maps) flows through a narrow gorge in Devonian and Carboniferous rocks from near the village of St. Nazaire de Ladarez, 22 kilometres north-north-west of Béziers, until it reaches a point one and a half kilometres south of the village. Near what is here termed the Upper Bridge (see Text-fig. 3) the river cuts through the lowest Devonian strata and enters a broader valley, the Landeyran Valley *sensu stricto* of geologists. This is excavated in relatively soft Ordovician mudstones and shales of the Arenig Series which are unconformably overlain by more resistant Devonian dolomitic limestones.

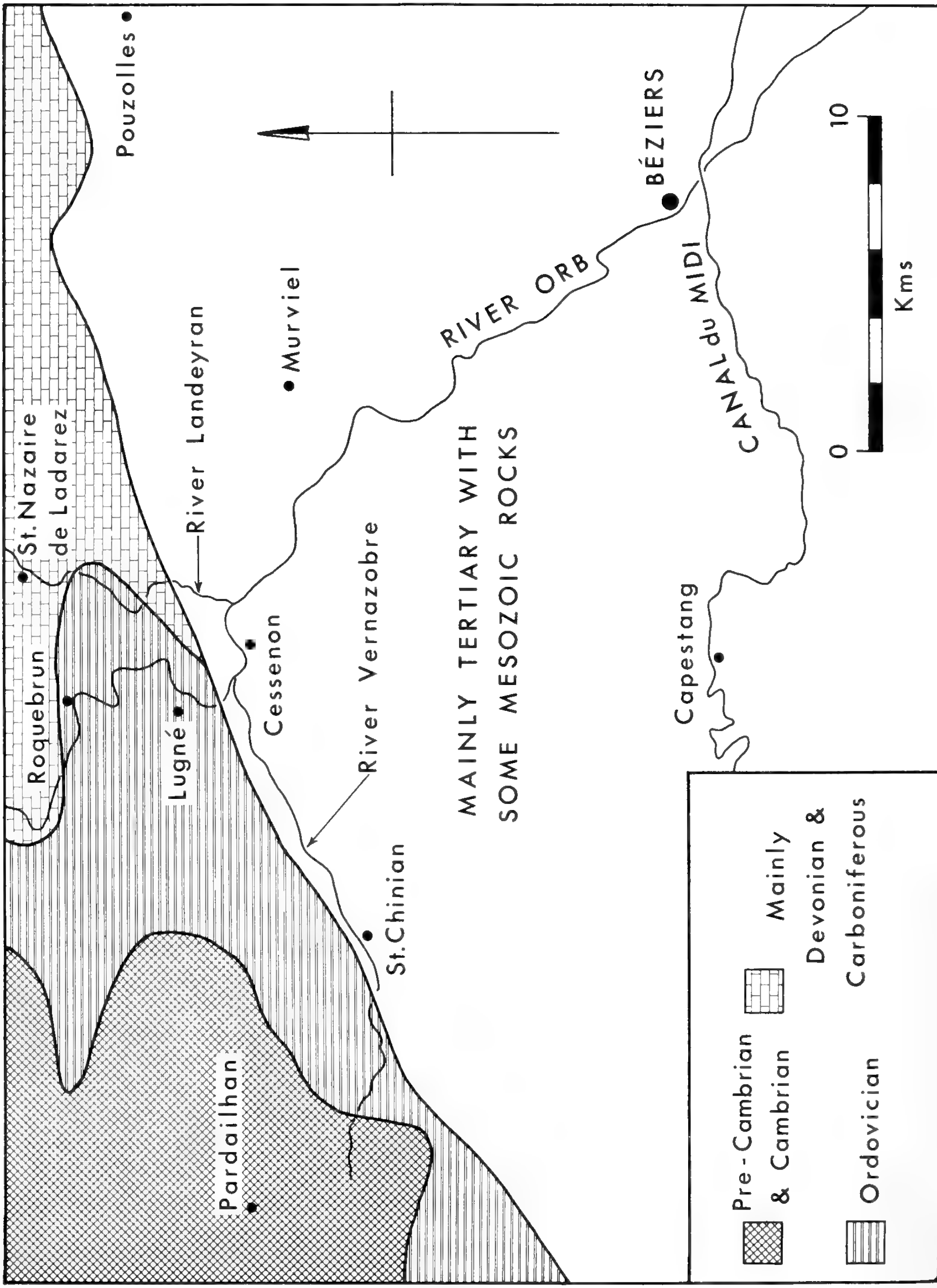

FIG. 1. Sketch-map showing part of the southern slopes of the Montagne Noire. The area described lies south-south-west of St. Nazaire de Ladarez.

The river follows an approximately south-south-westerly course for about two kilometres but then turns east-south-east at a point a few hundred metres upstream from Pont des Quatre Chemins, a bridge (see Text-fig. 3) marking the junction of the roads between St. Nazaire and Cessenon, and between Roquebrun and Causses-et-Veyran. Near the bridge the River Landeyran again intersects the Devonian outcrop and continues to join the River Orb, two and a half kilometres farther south. Apart from exposures in the bed of the river itself, the floor of the Landeyran Valley is mostly covered by Alluvium, extensively cultivated for the growing of vines. To the west of the valley the high, ridge-like feature of Serrelongue is composed of massive, yellow-weathering, often current-bedded sandstones, the Grès à Lingules, and these are underlain by conspicuously black, graptolitic shales, exposed in the Ruisseau de Setso (see Text-fig. 3) and referred to as the Schistes de Setso. The shales have yielded numerous specimens of *Didymograptus* as well as the trilobite *Taihungshania*.

Along the eastern side of Serrelongue runs the outcrop of the rocks succeeding the Grès à Lingules, a series of more flaggy sandstones and sandy shales discussed later under the name of Couches du Toulon. Most of the ground in this area is covered with thick maquis and examination of the strata is often difficult. The eastern margin of the Landeyran Valley is formed by massive, dolomitic limestones of Devonian age, the so-called " Mur Quartzeux " of French geologists. Owing to the large-scale and complex folding prevalent in this region, the strata here are vertical or even slightly overturned so that the Devonian beds, being more resistant than the adjacent Ordovician mudstones and shales, stand out as a parapet-like boundary, skirting the side of the valley and running east-north-east before curving westwards at both its northern and southern ends as mentioned earlier. The higher parts of the slopes formed by the Ordovician mudstones are generally covered with maquis whilst vineyards commonly occur on the lower slopes as well as over the alluvial flats.

The present paper deals mainly with the stratigraphy of the Ordovician rocks overlying the Grès à Lingules in the district between the River Orb near Le Foulon, north-east of Lugné, and the western margin of Mont Peyroux, south of St. Nazaire de Ladarez. In addition systematic descriptions are given of the numerous trilobites collected.

Detailed collecting was carried out by my wife and myself during the summers of 1961, 1962 and 1964, and I am indebted to the Trustees of the Godman Research Fund for financial assistance. Dr. Isles Strachan has identified all the graptolites found and commented on their geological horizons. Professor Avias and Monsieur M. Matte facilitated my examination of collections at the Geology Department of the University of Montpellier, whilst Professor M. Mattauer of the same university, who is engaged in remapping the geological structure of the region, supplied specimens and data collected by him and his students. Monsieur J. Destombes of the Service géologique du Maroc generously furnished information on the Ordovician rocks and faunas of the Anti-Atlas, as well as topotype specimens of *Calymene attenuata* Gigout. In Czechoslovakia Dr. R. Horný kindly allowed me to examine collections at the

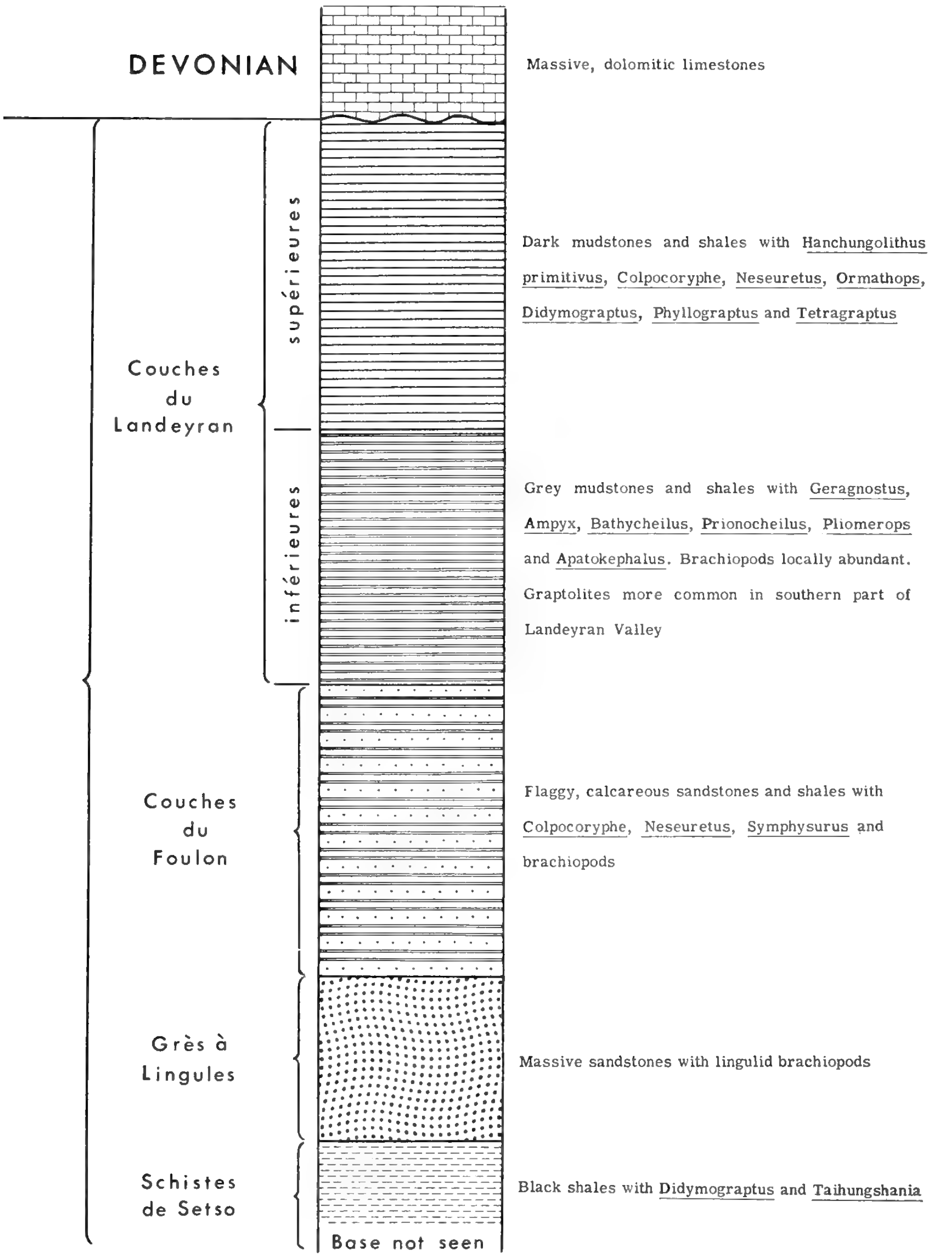

FIG. 2. Generalized succession of Ordovician rocks in the Landeyran Valley. Vertical Scale, 1 cm. = 40 m.

National Museum, Prague, and he, Dr. L. Marek and Mr. J. Vaněk supplied me with much useful information concerning Bohemian species. Finally, I am particularly grateful to the late Professor W. F. Whittard who, as on several previous occasions, kindly read and criticized the manuscript.

II. THE ORDOVICIAN SUCCESSION

Our detailed knowledge of the Ordovician stratigraphy of the Landeyran Valley arises from the researches of Thoral who first published a preliminary note (Thoral 1933) and soon afterwards put forward his ideas in more detail (Thoral 1935 : 490–494). He subdivided in descending order the strata succeeding the Grès à Lingules of the high ground of Serrelongue, from north-west to south-east, as follows.

4. Shales with *Phyllograptus angustifolius*, *Trinucleus primitivus*, *Dalmanites socialis*, *Dalmanites phillipsi*, *Dalmanella*.
3. Fossiliferous shales in vineyard on left bank of river, with *Calymene tristani*, *C.* cf. *aragoi*, *Trinucleus* cf. *primitivus*, *Didymograptus v-fractus*, *Phyllograptus angustifolius* and varieties.
2. Shales, sandy shales and nodules with *Didymograptus deflexus* and fragments of trilobites including *Homalonotus* (of Horizon 1) and *Symphysurus*, with *Redonia*, etc.
1. Grès à Lingules, overlain by black, sandy shales and siliceous nodules with micaceous sandstones. Fauna includes *Ogygia*, *Illaenus* and *Homalonotus* sp. nov.

Most of the extensive faunas collected by Thoral from the Tremadoc and early Arenig Series of the Montagne Noire were described by him in a large publication the same year (Thoral 1935*a*). The Arenig faunas had been obtained from the lowest part of that Series as interpreted by him, and their horizons fell within the so-called *Miquelina* (now *Taihungshania*) *miqueli* Zone, though one was from what are now termed the Schistes de Setso.

In a later paper Thoral (1941 : 140–141) gave the following succession for the Arenig Series in the region of the Orb Valley, particularly in the vicinity of the Landeyran Valley.

Schistes à *Phyllograptus* et à Trilobites (giving alternative names of Schistes de St-Nazaire or Schistes à Calymmene)
Schistes noirs de Setso
Grès à Lingules
Schistes psammitiques à *Didymograptus*
Schistes à *Miquelina miqueli* et *Vexillum*

In the same table Thoral used the terms " Schistes et grès à *Orthis* " and " Schistes du Foulon " for the strata succeeding the Grès à Lingules in the district of Le Foulon, but indicated some uncertainty as to their exact correlation.

The Cambrian and Ordovician agnostid trilobites of the Montagne Noire were described by Howell (1935) at about the same time that Thoral was describing the other shelly faunas, but the horizons, and sometimes localities, of some of the Ordovician forms were not known in great detail, and it was not apparent whether any of them were of stratigraphical value. Strangely enough, the faunas of the higher Arenig strata have remained largely undescribed. Similarly some of Howell's agnostids are now believed to be more restricted in their distribution than was once thought.

The most recent general account of the Lower Ordovician rocks in the Montagne Noire is that of Gèze (1949 : 42–46), though it does not deal with local details of stratigraphy. Gèze's map (1949, fig. 79) covering the neighbourhood of the Landeyran Valley indicated the strata above the Grès à Lingules as being subdivided into two parts. Generally speaking these were shown to occupy successively the western and eastern sides of the Landeyran Valley, forming a normal, undisturbed succession in the northern part of the valley and with their outcrops narrowing a little to the south-west, near Le Foulon. As will be explained later, such a hypothesis is not borne out by the present field observations. In his account of the Lower Ordovician stratal succession Gèze (1949 : 42) rightly stated that " Upper Arenig " and " Llandeilo " strata are absent from the district, but he adopted for the remainder of the Arenig Series a somewhat curious sequence in which certain of Thoral's (1941 : 140) local lithological subdivisions were elevated to the status of subzones within the *Didymograptus extensus* Zone, as follows :

Middle Arenig (=*Didymograptus extensus* Zone)	Subzone of *Didymograptus protobifidus* and *Phyllograptus angustifolius* Subzone of *Didymograptus deflexus* and *D. balticus* Subzone of *Didymograptus v-fractus*
Lower Arenig	Zone of Dichograptidae and Dendrograptidae Sandy shales with *Vexillum* and *Miquelina miqueli*

The definition of the Arenig Series and the graptolite zones constituting it have recently been reviewed by both Bulman (1958 : 164–165) and Whittard (1960 : 17–19). The zones into which this series is customarily divided derive primarily from the work of Elles (1904 ; 1922) and comprise, in ascending order, the two zones of *Didymograptus extensus* and *D. hirundo*. On the basis of her later work on the Skiddaw Slates of the English Lake District, Elles (1933 : 100–102) further subdivided the Arenig and higher Tremadoc Series as shown below. Bulman (1958 : 164) has pointed out that there is no evidence for the existence of a separate *Dichograptus* Zone, and has also cast doubt on the validity of the *Tetragraptus* Subzone, asserting that no concentration of *Tetragraptus* occurs at the base of the Arenig Series. He has, however, maintained the validity of the three topmost subzones of the Extensus Zone, but unfortunately it has not proved possible to apply these to the strata of the Landeyran Valley region, where the zone is not subdivided.

Series	Zone	Subzone
Arenig	*Didymograptus hirundo*	
	Didymograptus extensus	*Isograptus* [*Didymograptus*] *gibberulus* *Didymograptus nitidus* *Didymograptus deflexus* Upper subzone of *Tetragraptus* (reclined)
Tremadoc	*Dichograptus*	Lower subzone of *Tetragraptus* (horizontal)
	Bryograptus kjerulfi	

In the present paper the following succession is adopted for the Ordovician rocks below the unconformable Devonian in the vicinity of the Landeyran Valley.

Couches du Landeyran { Couches supérieures / Couches inférieures }
Couches du Foulon
Grès à Lingules
Schistes de Setso

(*a*) *Schistes de Setso and Grès à Lingules*

The well-known occurrence of black, graptolitic shales in the stream-section of the Ruisseau de Setso, some 600 metres west of the River Landeyran, marks the lowest Ordovician horizon of the immediate district. Their total thickness, though not known with certainty, is probably small. At one time Thoral (1935 : 490) stated that the Schistes de Setso were the lateral equivalent of part of the Grès à Lingules. Later, however, he placed them stratigraphically higher than that horizon (Thoral 1941, table on pp. 140, 141). Such an interpretation is not supported by the various sections along the western side of the Landeyran Valley, and from his recent researches Professor Mattauer informs me (personal communication) that he regards the Schistes de Setso as being stratigraphically below the Grès à Lingules, a conclusion with which I agree. Fossiliferous shales form an outcrop in the Ruisseau de Setso about 1,250 metres north-north-west of Pont des Quatre Chemins. This section provided the various fossils noted by Thoral in his publications and was, in fact, marked by him as a fossil locality on the second edition of the 1 : 80 000 Bédarieux Sheet (Blayac *et al.* 1938). According to Thoral (1935*a* : 258) the Schistes de Setso, which yielded the type material of *Taihungshania miqueli* (Bergeron) *landayranensis* (Thoral), contain the graptolites *Didymograptus v-fractus* Salter and *D. v-fractus* var. *volucer* Nicholson. In Britain the two last-named occur in what Elles & Wood (1914 : 516) called the *Dichograptus* Zone and *Didymograptus extensus* Zone of the Arenig Series, and even though the *Dichograptus* Zone has been shown by Bulman (1958 : 164) to be non-

existent, an early Arenig age is evidently indicated. My own collection from the Schistes de Setso contains numerous didymograptids identified as *Didymograptus* cf. *deflexus* Elles by Dr. Strachan who regards them as indicative of the Extensus Zone.

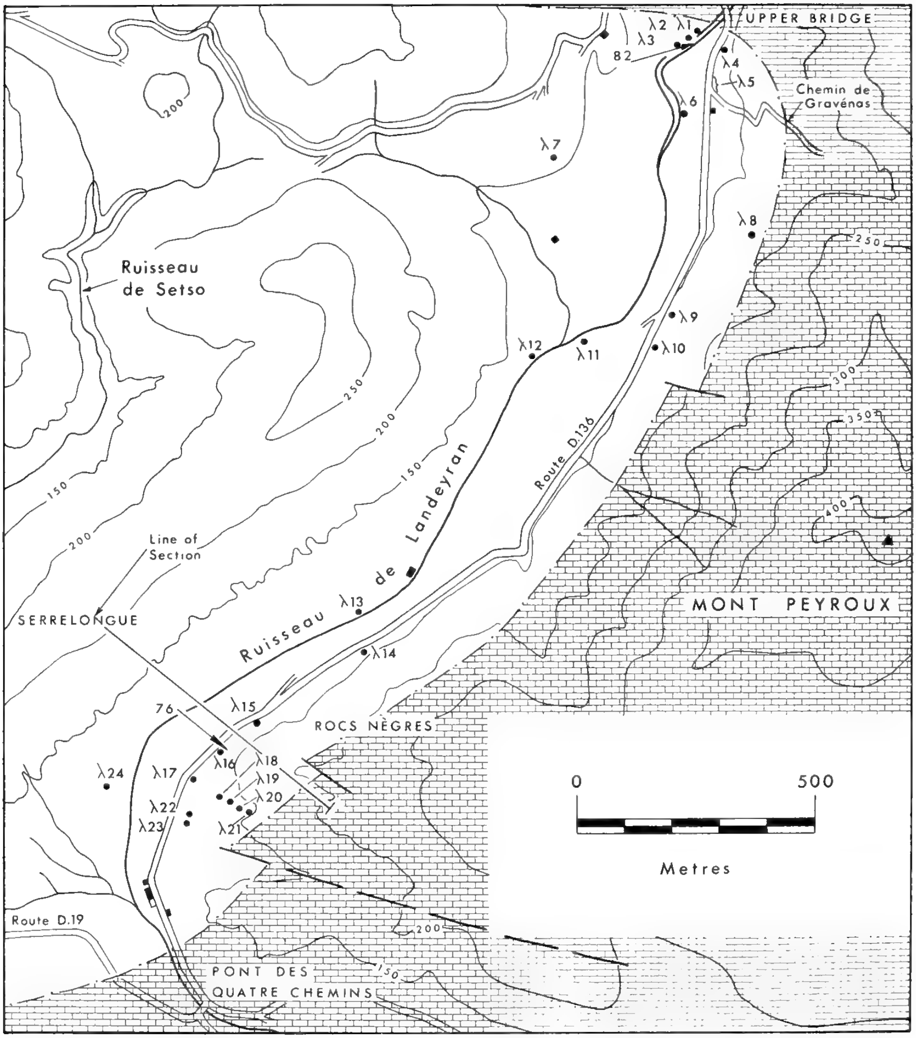

FIG. 3. Outline map showing principal fossil localities in the Landeyran Valley. Height of contours in metres. The l'Escougoussou district (see Text-fig. 5) lies beside Route D.19 immediately south-west of this map. Ordovician outcrop unshaded; brick-pattern denotes Devonian/Carboniferous rocks.

The Grès à Lingules comprise a series of massive, often impersistent sandstones and quartzites, frequently exhibiting shallow-water characteristics and having an estimated thickness of about 90 metres or more in the vicinity of Serrelongue. Apart from occasional occurrences of inarticulate brachiopods (*Lingula* s.l. and *Dinobolus*), most of the rocks are unfossiliferous and there is no evidence of their age with reference to the graptolite zones. Previous records of *Lingula crumena* Phillips from these strata are certainly mis-identifications, since the species occurs typically in the Lower Silurian (Llandovery Series) of England and Wales.

Thoral (1935 : 174) regarded the Grès à Lingules as being, without any doubt, equivalent to part of the "grès armoricains" of Brittany. It is tempting to equate such generally similar sandstone successions, but dangerous when dealing with shallow-water deposits, even over relatively short distances, not to mention the 700 or so kilometres between Brittany and the Montagne Noire. In practice there is no stratigraphical evidence to sustain Thoral's claim. The Grès à Lingules are known now to be of early Arenig age, whilst the Grès armoricain is overlain by the true Schistes à Calymènes, belonging to the *Didymograptus murchisoni* Zone, the upper graptolite zone of the Llanvirn Series (Dangeard 1951 : 46). It seems likely, therefore, that the Breton strata are no older than the lower part of the Llanvirn or the upper part of the Arenig Series.

(*b*) *Couches du Foulon*

The top of the Grès à Lingules is marked by the appearance of a series of flaggy and less massively-bedded sandstones, some of them with calcareous bands, and intercalated, grey, micaceous, sandy shales. The fauna is more varied than that from the underlying Grès à Lingules and the beds are grouped here to form a new stratal sub-division, the Couches du Foulon, which should not be confused with the old

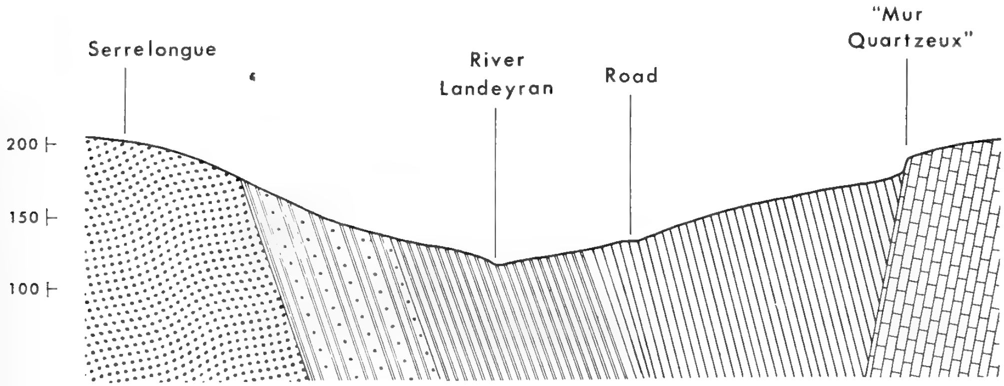

FIG. 4. Transverse (NW–SE) section showing the Ordovician succession in the southern part of the Landeyran Valley. Heights in metres. Scale, 1 cm = 50 m. For key to succession see Text-fig. 2.

name " Schistes du Foulon ". The latter was never adequately defined, though it was probably applicable to strata listed and described in the present account as the Couches du Landeyran inférieures, and its continued use seems inadvisable.

Thoral (1933 : 147), in discussing the Ordovician rocks of the Landeyran Valley, noted alternating sandstones and sandy shales with siliceous nodules overlying the Grès à Lingules. The same fauna was said to be found in the sandstones and the nodules, and to include " *Calymene* sp., *Asaphus* sp., *Orthoceras*, *Orthis*, *Redonia*, etc.". The beds were described by Thoral as being followed stratigraphically by blackish, sandy, micaceous shales, forming the southern flank of Serrelongue and containing the same fauna as before with the addition of crinoids and *Didymograptus*. The estimated maximum thickness of the Couches du Foulon is about 160 metres.

In geological papers dealing with the Montagne Noire frequent allusion is made to the district known as Le Foulon, but little detailed information and no large-scale geological map of the Ordovician succession have been published. Although the building marked as Le Foulon on the latest edition of the Saint Chinian Sheet of the Carte de France stands by the west bank of the River Orb, some 1,300 metres east of the village of Lugné, the district known by that name in much of the literature lies adjacent to the east bank of the river, about one and a half kilometres south-west of Pont des Quatre Chemins. A map published by Carles (1895) in an excursion guide to the district showed what were termed the " Terrasses du Foulon ", a name used for the so-called " meadows ", an area of marshy ground, by the east bank of the Orb where that river turns westwards towards Lugné. The name Le Foulon was applied originally to the now disused building and its associated system of aqueducts and outbuildings situated immediately by the east bank of the River Orb some 700 metres downstream from the Usine Maynard (see Text-fig. 5). This usage is retained for the present account.

The " Mur Quartzeux " of the unconformable Devonian rocks sweeps across the course of the River Landeyran near Pont des Quatre Chemins, skirts the lower hill slopes south of l'Escougoussou (fringing the high ground known as Puech Pus), and continues south-westwards until it stops just short of the River Orb, across the river from Lugné. A transverse section running roughly east-west through Lugné to near Siala by way of the Le Foulon district was published by Miquel (1895). This showed the Grès à Lingules followed successively by shales which were equated with the " Schistes de Boutoury ", the whole being overlain by the Devonian " Mur Quartzeux ".

The only detailed account of the Ordovician strata in the Le Foulon district is that of Thoral (1941 : 123). His findings are important, particularly with reference to the strata just above the Grès à Lingules (that is, the Couches du Foulon), and may usefully be summarized here. A traverse made in a north-south direction from the River Orb near Le Foulon along the bed of the stream flowing to the Orb from the Col de Siala produced the following succession, measured from the edge of the river's Alluvium. The dip of the beds was said to be south-south-east to east-south-east, and successively higher Ordovician strata were listed southwards to the unconformable Devonian " Mur Quartzeux ".

DEVONIAN

Ordovician/Devonian junction masked by talus

Thick series of black shales with sandy bands situated at points 25 and 50 metres south of the Grès à Lingules outcrop. Beds dip at 55 degrees.	No thickness given
Slightly quartzose shales with hard calcareous nodules. Numerous fossils, but only undistorted in nodules. *Ogygia*, orthoceratids, *Orthis* (small), crinoids, etc.	1 to 2 metres
Alternating shaly and sandy beds	6 metres
Sandy black shales	1·5 metres
Dark sandstones, in thin beds	4 metres
Grès à Lingules in beds up to 1 metre thick with *Lingula lesueuri*. Shell bed of lingulids (3 cm. thick) near top of formation.	10 metres

The unconformable Devonian outcrop runs close to the River Orb near Le Foulon, just skirting the track leading from the Usine Maynard to Siala, but the Ordovician/Devonian junction is obscured by rock débris and vegetation. However, between the track and the river, particularly just downstream from Le Foulon, the alternating shales and sandstones of the Couches du Foulon are fairly well exposed. Still farther to the south-west the track to Siala forks, and near this point the highest Couches du Foulon are seen, dipping east at 40° and overlain by the Couches du Landeyran inférieures (for an account of these beds, see p. 265). The larger, south-easterly branch of the track continues up the hillside, at first almost following the strike of the sandstones and shales but then passing lower in the succession. West of the track at this point is the small, generally dry, valley which runs northwards to the River Orb from the high ground north-west of Siala, and in it the Couches du Foulon are well exposed. The outcrop of these strata continues south-westwards along the strike and occupies most of the hill formed by Ordovician rocks north-west of Vessas, where they are faulted against the Tertiary to the south-east (Gèze 1949, fig. 79).

In recent years Gigout (1956 : 2739–2740) has mentioned an unsorted collection made by Thoral from the " Middle Arenig " of the Landeyran Valley (the term Arenig being used by Thoral (1941 : 140) to comprise the lower Llanvirn Series in addition to the Arenig *s.s.*). Gigout noted the resemblance of the fauna to one he himself had described earlier (1951) from the region south-west of Casablanca, containing " *Calymene attenuata* Gigout, *Calymene* aff. *pulchra* Hawle & Corda and *Calymenella* aff. *media* (Barrande)." By kind permission of Professor Avias I have examined at Montpellier the Thoral collection cited by Gigout. Assembled in about 1932 the material, which is not yet sorted, is labelled as coming from the " Toit des Grès à Lingules " (that is, strata forming part of the present Couches du Foulon) at an unspecified locality said to be " near Pont de St. Nazaire ", though this name appears to have been used indiscriminately in some older collections to denote either of the two bridges in the Landeyran Valley. The rock is a yellow-weathering,

decalcified sandstone, part of which contains an abundant shelly fauna consisting in the main of brachiopods and trilobites. The latter mostly comprise disarticulated asaphids with *Neseuretus* and *Symphysurus*. The exact position of Thoral's locality has not yet been rediscovered, and outcrops of this horizon in the southern part of the Landeyran Valley are singularly unproductive, though the area is large and collecting often difficult. However, near the northern end of the valley, at locality $\lambda 7$, massive and flaggy sandstones with some calcareous bands and shales were examined, the whole being well-jointed and the shales slickensided. The more calcareous bands yielded poorly-preserved *Colpocoryphe*, *Neseuretus* and a few brachiopods. No other fossil localities have yet been found in these strata within the limits of the map shown in Text-fig. 3.

(c) *Couches du Landeyran*

Although bands of sandy, micaceous shale are found intercalated with the flaggy sandstones of the Couches du Foulon, they have not proved fossiliferous in the present instance and are often slickensided. The following account of the Couches du Landeyran deals, therefore, only with the succeeding, more or less continuous, sequence of dark mudstones and shales. These contain occasional siliceous nodules and concretionary bands sometimes exhibiting " cone-in-cone " structure. The rocks are mostly dark grey or grey-green in colour, though the shales of the Couches inférieures are generally a paler grey. Graptolites are sometimes preserved in relief, especially in light grey shales low in the succession, but are often pyritic films in the darker beds. " Shelly " fossils occur mostly in the darker strata, occasionally with part of the calcareous shell preserved but generally in the form of ochreous internal and external moulds with the intervening space filled by an amorphous mass of orange, limonitic material. Although fossils were generally found scattered throughout the succession, in some cases they were collected from thin bands which showed signs of sorting.

The shelly faunas are of a composition broadly similar to that of many other Lower and Middle Ordovician successions of dark mudstones and shales, for example those of Bohemia, the Iberian Peninsula, north-western France, and the Anglo-Welsh area (see pp. 345–348). They consist mainly of trilobites, the dominant groups present being trinucleids, dalmanitids and asaphids, with subsidiary, though important, agnostids, calymenids (*s.l.*) and raphiophorids. Molluscs are generally abundant, particularly bivalves such as *Redonia*, as are supposed phyllopods (*Ribeiria*) and hyolithids, but brachiopods are usually uncommon, apart from a few localized occurrences with numerous shells occurring in bands.

The section near Le Foulon (see p. 258) was claimed by Thoral (1941 : 124) as the only one that could be followed bed by bed upwards from the Grès à Lingules. The so-called fossiliferous " Schistes du Foulon " were said to be absent there, though they were described as cropping out a little farther east, at the margin of the cliff formed by the Devonian " Mur Quartzeux ", between it and the road which, coming from Le Foulon, "connects the meadows situated downstream ". Thoral said that

the relationships of the " Schistes du Foulon " were thus difficult to distinguish. They followed above the black shales of the section taken at the eastern side of the outcrop described above, and should be found under the scree or were covered by the transgressive Devonian rocks. The succession is discussed later in this chapter. According to Thoral, on following the Ordovician/Devonian junction the " Schistes du Foulon " appeared either to pass laterally into the " Schistes à *Phyllograptus* " (now Couches du Landeyran supérieures) of Le Touraillas (a locality in the Landeyran Valley ; see p. 258) or to rest upon them. Thoral noted, however, that isoclinal folds could exist within the Ordovician shales and suggested that the " Schistes du Foulon " should be placed at least 100 metres, and probably 200 metres, above the Grès à Lingules.

Graptolites were said to be both rare and of little variety, all being of the tuning-fork type and belonging to the *protobifidus/bifidus* group of *Didymograptus*. On account of the similar graptolites in the " *Phyllograptus* Beds " of Le Touraillas, and the supposed affinity between the trilobite faunas of the " Schistes du Landeyran " and the " Schistes du Foulon " Thoral concluded that both formations were of approximately the same age, and that both were slightly higher than the *Didymograptus deflexus* Subzone. His results were summarized in a table (Thoral 1941 : 140–141) as follows :

		Middle Valley of the Orb	
		Le Foulon	Le Landeyran
Didymograptus extensus Zone	Subzone of *D. gibberulus*	?	Shales with *Phyllograptus* and trilobites
	,, ,, *D. nitidus*	Schistes du Foulon	
	,, ,, *D. deflexus*	Shales and sandstones with *Orthis*	
		—— —— —— ——	Black shales of Setso
	,, ,, *Tetragraptus* (reclined)	Grès à Lingules	Grès à Lingules
		?	

Elsewhere, in a paper devoted mainly to the Silurian and topmost Ordovician rocks of Languedoc, Thoral (1941*a*, table) listed the following succession for the Ordovician strata of the middle valley of the River Orb :

Schistes du Foulon à *Didymograptus protobifidus*
Schistes de St. Nazaire à *Phyllograptus*
Schistes de St. Nazaire à *Didymograptus defluxus* [sic]
Grès à Lingules
Grès et schistes à nodules de l'Arénig inférieur et du Trémadoc.

No reasons were given for this assignment of the beds at Le Foulon to an horizon stratigraphically higher than the strata of the Landeyran Valley, and such a sequence can no longer be sustained.

(*i*) *Couches du Landeyran inférieures*

The Landeyran Valley

At the northern end of the Landeyran Valley, almost 200 metres downstream from the Upper Bridge, there is a right-angled bend in the course of the river (see Text-fig. 3). At this point almost vertical, or even slightly overturned, massive and flaggy sandstones of the Couches du Foulon are well exposed in the western bank of the river. They are succeeded downstream by Couches du Landeyran inférieures, sometimes with brachiopods (for example at λ6), whilst immediately upstream they appear to be separated by a small fault from further outcrops of the Couches inférieures which can then be followed successively upwards towards the Upper Bridge. Apart from occasional outcrops most of the eastern bank of the river is occupied by Alluvium, but the higher western bank and the river bed exhibit a fairly continuous succession, which is taken as the type-section of the Couches inférieures. The section is best examined in late spring and summer when the flow of river water is almost non-existent. The rocks mostly comprise strongly jointed and often highly compacted mudstones, and the clockwise rotation of the strike observed as followed southwestwards from the Upper Bridge is attributable to subsidiary folding of the less competent Ordovician strata within the large overfold of the Devonian " Mur Quartzeux ". The Couches inférieures in the northern part of the valley vary in colour from light or dark grey to purple and contain sporadic concretionary bands which sometimes exhibit cone-in-cone structure. The lower strata of the section south-west of Upper Bridge did not prove particularly, or diagnostically, fossiliferous but a fossil-band at λ3 yielded fragments of large asaphid trilobites in a dark grey micaceous mudstone. Farther towards the bridge, however, the strata become more fossiliferous and faunas were collected at λ1 and λ2, particularly the latter. At λ2, in the north-western bank of the river, fossils were found fairly commonly through about one metre of rock, and a thin (15 cm.) horizon yielded an interesting assemblage of trilobites and brachiopods. The former include *Geragnostus*, *Apatokephalus*, *Bathycheilus*, *Colpocoryphe*, *Pliomerops*, *Prionocheilus* and asaphid fragments. Brachiopods at λ2 include a few lingulids and more common dalmanelloids, the latter being found in still greater abundance some 20 metres upstream, in grey shales exposed in the north-western bank at λ1. No other significant fossiliferous horizons were found between λ1 and the Devonian unconformity near the Upper Bridge, but a fauna broadly similar to that of λ2 was examined by the roadside at λ5. At this point, by the eastern side of the road some 24 metres south of its intersection with the Devonian unconformity, several bellerophontid gastropods, including *Sinuites*, were found in association with *Apatokephalus*, *Colpocoryphe* and asaphid fragments, some of large size. Another locality (λ6), in the south-eastern bank of the river yielded several brachiopods and its horizon may not be far removed from that of λ1. The strike of the beds brings these northernmost Couches inférieures to the track-section in the western part of the Chemin de Gravénas and beneath the adjacent vineyards, where fragments of fossiliferous mudstone are often turned up by the plough.

Additional and numerous exposures of the Couches inférieures were examined in the

area about 450 metres south of the Upper Bridge, both near the roadside and on the hill-slopes to the east, where the beds are overlain by the Couches supérieures at and near λ8 (see p. 269). Fossils may be locally abundant but are badly preserved and consist mainly of gastropods and bivalves. Similar strata occur still farther south near localities λ9 and λ10 as well as to the south-west, both in the river bed (localities λ11 and λ12) and in the stream which joins the River Landeyran from the north-west (see Text-fig. 3). In and near the stream section are large exposures of the Couches inférieures, here almost unfossiliferous and strongly jointed, which may be traced north-westwards as far as their junction with the underlying Couches du Foulon, some 250 metres north-west of the stream/river intersection.

The mudstones and shales of the Couches inférieures along and to the west of the western bank of the River Landeyran still farther south proved to be almost barren, yielding only poorly-preserved bivalves, gastropods and fragmentary asaphids. The lowest beds are poorly exposed, being covered by thick maquis, but the thickness of the Couches inférieures in this area has been estimated at about 140 metres. The outcrop around locality λ24 (see Text-fig. 3) is dissected by some small, dry stream-courses which facilitated the collecting of the few available fossils. These included the almost ubiquitous gastropods and bivalves together with a few brachiopods, an assemblage generally similar to those found at the northern end of the valley.

The l'Escougoussou district

About 600 metres west-north-west of Pont des Quatre Chemins lies the farm known as l'Escougoussou, by the north side of the road (Route D.14) leading from Murviel, *via* the bridge, to Roquebrun. The road from the Landeyran Valley to the Orb Valley attains its highest point here and passes through a large " notch " eroded in the shales and mudstones cropping out between the more resistant masses formed by the Grès à Lingules of Serrelongue (to the north) and the Devonian " Mur Quartzeux " of Puech Pus (to the south). The main farm-building borders the northern side of the road, and opposite its western end is a large exposure of what are apparently Couches du Foulon, in the steep, southern side of the road. The rocks, which comprise massive and flaggy sandstones with subsidiary shales, dip steeply south-eastwards and have not yet yielded recognizable fossils. They are followed stratigraphically by part of the Couches du Landeyran inférieures, here a series of shales and mudstones, pale, greenish-grey in colour and with a steep, variable dip to the south-east. The beds are often slickensided and weathered, tending to crumble easily, so that fossil-collecting is difficult. Exposures occur along both sides of the road, particularly the southern side, for a distance of more than a hundred metres, and fossils may be found throughout most of the visible succession. Their state of preservation is not generally good, however, but the localities which proved most profitable are shown in Text-fig. 5. The fauna is essentially graptolitic. Pendent didymograptids are the most common forms, with an occasional tetragraptid. Non-graptolitic fossils are uncommon but include occasional trilobites (asaphid fragments and *Colpocoryphe?* sp. indet.), a few brachiopods (including lingulids and

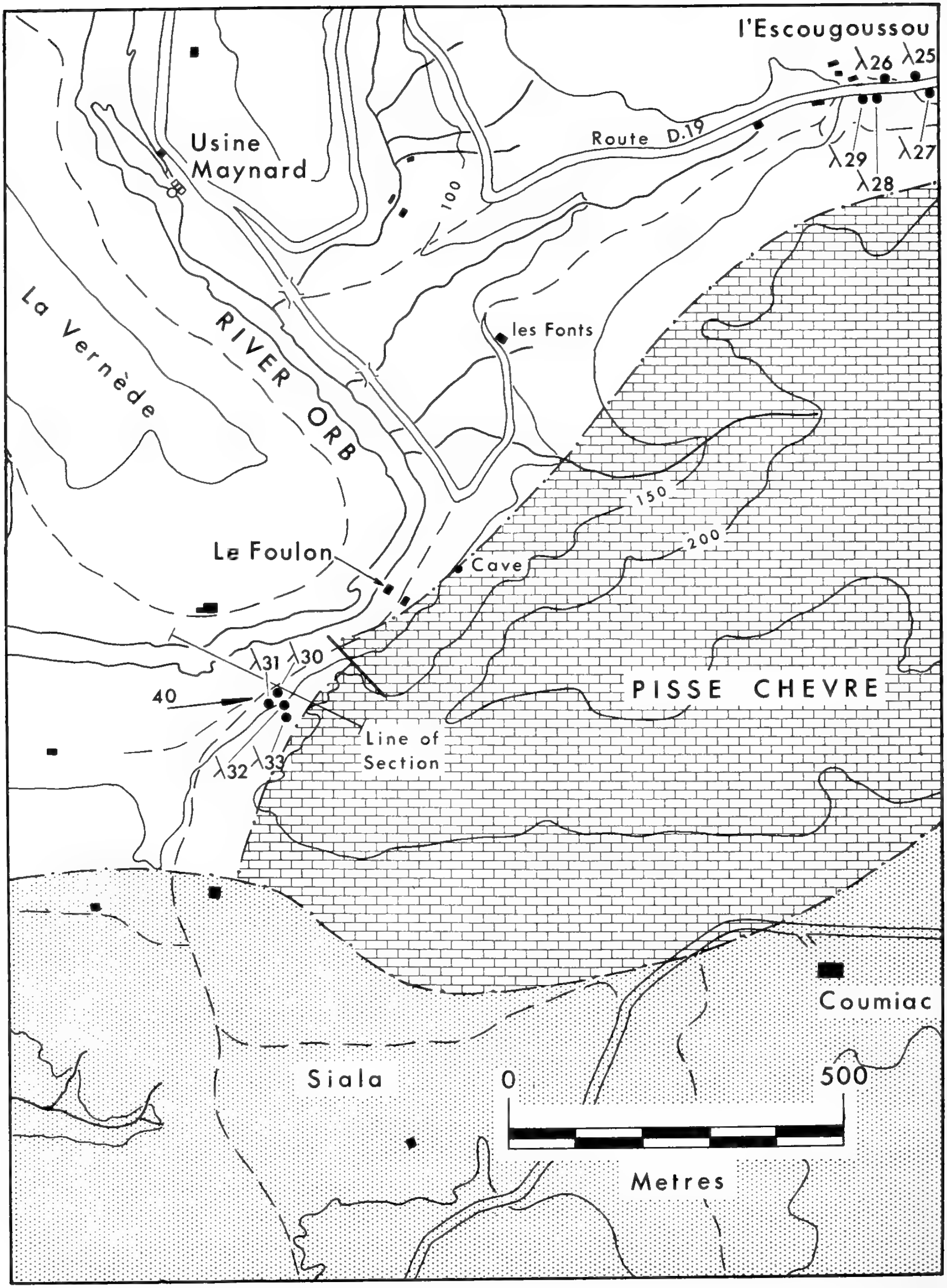

FIG. 5. Sketch-map showing fossiliferous localities in the Couches du Landeyran inférieures near l'Escougoussou and south-west of Le Foulon. The shaded area around Siala represents the Tertiary outcrop; the Devonian/Carboniferous rocks are denoted by the brick-pattern; the Ordovician outcrop is unshaded.

dalmanelloids), with *Ribeiria*, *Redonia* and some poorly-preserved gastropods. The graptolites have been examined by Dr. I Strachan whose determinations are shown below. He considers the shaly succession here to belong to the *Didymograptus extensus* Zone.

	Graptolite Localities				
	λ25	λ26	λ27	λ28	λ29
Didymograptus sp.	×	×	×	—	—
Didymograptus? sp.	—	—	—	—	×
Tetragraptus pendens Elles?	—	—	—	×	—
Tetragraptus? sp.	—	—	×	—	×

It is interesting to note a certain lack of correspondence between the mudstones of the Couches inférieures at the northern and southern ends of the Landeyran Valley. The mainly graptolitic strata of l'Escougoussou do not, as far as we know, have counterparts near the Upper Bridge. Conversely, the trilobitic strata of λ2 and its vicinity have not yet been found near l'Escougoussou. However, the relationships may be obscured by both structural complications as well as by the Alluvium.

The district near Le Foulon

The Usine Maynard (or Moulin Maynard as it is shown on certain maps) is situated by the eastern bank of the River Orb some two kilometres north-east of the village of Lugné and about one kilometre west-south-west of the farm l'Escougoussou. About 700 metres south-south-east of the Usine Maynard is the section through what are now the Couches du Foulon which was described by Thoral (1941 : 123). Above these strata are found outcrops of the present Couches du Landeyran inférieures, that is to say mudstones and shales to which the name " Schistes du Foulon " has previously, and loosely, been applied. No detailed map or faunal list has been published for the district, a curious omission in view of the allegedly fossiliferous strata there and the attempts made to correlate them with other beds. Thoral (1941 : 125) claimed that there was a strong analogy between the trilobitic faunas of what he called the " Schistes du Landeyran " and the " Schistes du Foulon ". He concluded that both horizons were of approximately the same age, higher than the *Didymograptus deflexus* Subzone, and represented the upper part of the " Middle Arenig ". Referring to his " Horizon 4 " in the Landeyran Valley (now equal to at least part of the Couches du Landeyran supérieures) Thoral (1935 : 493) stated that between the " *Phyllograptus* horizon " and the Devonian there occurred grey-green shales in which no determinable fossils were found. He concluded that these might " represent the Upper Arenig and Llandeilo as at Le Foulon ", though there was no palaeontological proof. His hypothesis introduced complications of large lateral variations of faunal facies which do not appear to exist, and must now be abandoned.

The Couches du Landeyran inférieures are best exposed in the Le Foulon district in the steep hillside between the Devonian " Mur Quartzeux " and the track from the Usine Maynard to Siala, at a point about 250 metres south-west of the true Le Foulon and above the fork in the track some 750 metres south-south-east of the

Usine Maynard. The rocks comprise dark, grey-green mudstones and shales, deeply weathered so that the section is obscured by a scree of fine shale fragments. In consequence the fossils, which tend to be found concentrated into thin bands, are not always easy to find. They may, however, be locally abundant and it is reasonable to suppose that the old collections labelled merely " Le Foulon " originated here. Most of the section was sampled and four principal fossiliferous horizons were found. Additional fossil-bands probably exist but they are difficult to find owing partly to the degrees of weathering and partly to their own impersistent nature. The succession of the Couches du Landeyran inférieures in this section is summarized below (Text-fig. 7). There is room here for a total thickness of approximately 50 metres, and the horizons of the principal fossil localities are shown, but the thickness farther south may be greater. The fauna is more abundant than at the corresponding level in the Landeyran Valley, and a particularly interesting feature is the distribution of *Bathycheilus gallicus*, here ranging through most of the succession whereas it has been found at only one locality near the Upper Bridge.

Although the poor exposures make it difficult to demonstrate the fact, the outcrop of the Couches du Landeyran inférieures widens slightly to the south-west of the hillside section just described and narrows north-eastwards near Le Foulon. Still farther north-east the ground is again poorly exposed and the beds are not seen clearly again until the vicinity of l'Escougoussou is reached.

The section of the Couches du Landeyran inférieures near Le Foulon is of particular interest in two respects. First, it illustrates once again the folding of the Arenig strata beneath the Devonian unconformity, so that the Couches du Landeyran supérieures have been eliminated by overstep at Le Foulon, as they have at the northern end of the Landeyran Valley. Secondly, it shows the striking resemblance between the shelly faunas of the Couches inférieures at Le Foulon and in the north

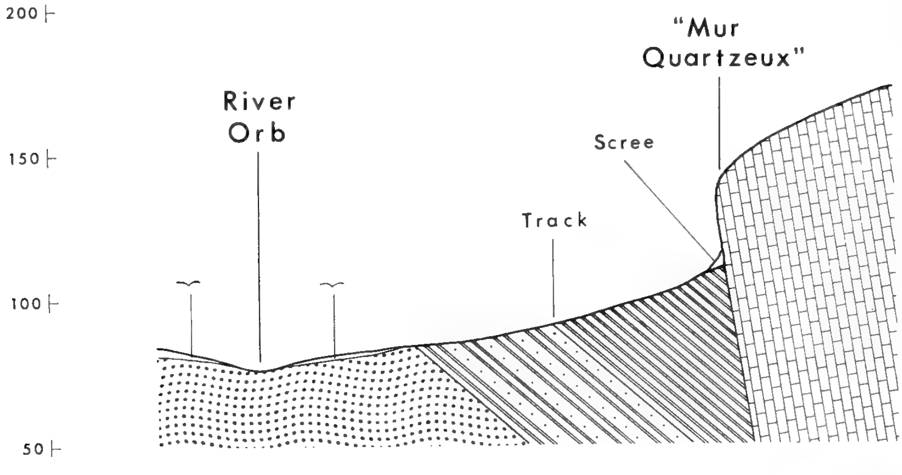

FIG. 6. Transverse (WNW–ESE) section showing the relationship of the Ordovician and Devonian rocks south-west of Le Foulon. For key, see Text-fig. 2. Scale, 1 cm. = 25 m.

of the Landeyran Valley, even though the equivalent faunas of the intervening l'Escougoussou area are very different. I have not yet examined in detail the Ordovician outcrops of the Boutoury district, near Cabrières, but the old collections at Montpellier University contain numerous trilobites from there. Several of the characteristic forms of the Couches inférieures (and also the Couches supérieures) are represented and their matrix does not differ significantly from that of the Landeyran–Le Foulon district. The distribution of trilobites, as known at present, is shown in tabular form below. In order to convey some idea of the relative abundance of the different genera and species, the following, purely arbitrary convention is used. Very common = 10 or more specimens ; Common = 7–9 specimens ; Uncommon = 4–6 specimens ; Rare = 1–3 specimens ; a dash indicates that the genus has not yet been found. For the column dealing with the Boutoury district, a cross merely shows that the genus is known in museum collections.

	Northern end of Landeyran Valley	Le Foulon	Boutoury
Ampyx	Rare	Uncommon	×
Apatokephalus	Uncommon	Very common	×
asaphids	Very common	Very common	×
Bathycheilus	Common	Very common	×
Ceraurinella	—	Rare	—
Colpocoryphe	Common	Very common	×
Geragnostus	Uncommon	Very common	×
Ormathops	—	Rare	—
Pliomerops	Rare	—	×
Prionocheilus	Common	—	—
Selenopeltis	—	Rare	—

(*ii*) *Couches du Landeyran supérieures*

The highest members of the mudstone succession in the Landeyran Valley are generally better defined, in terms of faunal content, than the Couches inférieures. These topmost strata, which he termed " Horizon 4 ", were discussed briefly by Thoral (1935 : 492–493). " Horizon 4 " constitutes all, or at least part of, what are now called the Couches du Landeyran supérieures. Thoral followed Born (1921) in regarding the shelly faunas of these beds as being " stratigraphiquement neutres " and therefore of little use compared with the graptolites, as they were thought to include species ranging from the Arenig to the Llandeilo Series. Born's original faunal list, however, is now known to contain numerous misidentifications, and Thoral's pessimism can no longer be shared. Perhaps the most conspicuous feature is the incoming of trinucleid trilobites, a group which otherwise is poorly represented in the Ordovician rocks of the Montagne Noire. All the specimens so far found belong to the genus *Hanchungolithus* Lu 1954, and to the species *Hanchungolithus* [*Trinucleus*] *primitivus* (Born), recently redescribed by Whittard (1957) as *Myttonia*

primitiva. The Couches du Landeyran supérieures form a considerable outcrop along the south-eastern side of the Landeyran Valley, particularly in the type-section about 400 metres north of Pont des Quatre Chemins, and have an estimated thickness of approximately 170 metres. The lateral extension of these strata elsewhere in the Montagne Noire is indicated by the presence, in older collections at Montpellier University, of several specimens of *Hanchungolithus primitivus* from Boutoury, about 25 kilometres to the north-east.

In his various publications dealing with the district around the Landeyran Valley, Thoral frequently alluded to a locality known as " Le Touraillas " or " Le Toaraillas " (for example, Thoral 1941 : 122). No such place is shown on the map of the area but from Thoral's account, and his mention of " la falaise schisteuse du Touraillas ", it appears that he was probably referring to the section to the south-west of Rocs Nègres, some 600 metres north-north-east of Pont des Quatre Chemins. This is the type-section of the Couches du Landeyran supérieures, which are well exposed there.

By the eastern side of the St. Nazaire road about 440 metres north of Pont des Quatre Chemins is a large exposure (see Text-fig. 3, locality λ17) where mudstones and shales have been quarried. This is the type-locality of *Trinucleus primitivus.* It was cited by Spjeldnaes (*in* Whittard 1957) who, on the basis of graptolites found there, suggested that the horizon probably formed part of the Llanvirn Series, though Whittard (*loc. cit.*) noted that *Myttonia,* the genus to which he then assigned *Trinucleus primitivus,* was known only from the Arenig Series in West Shropshire.

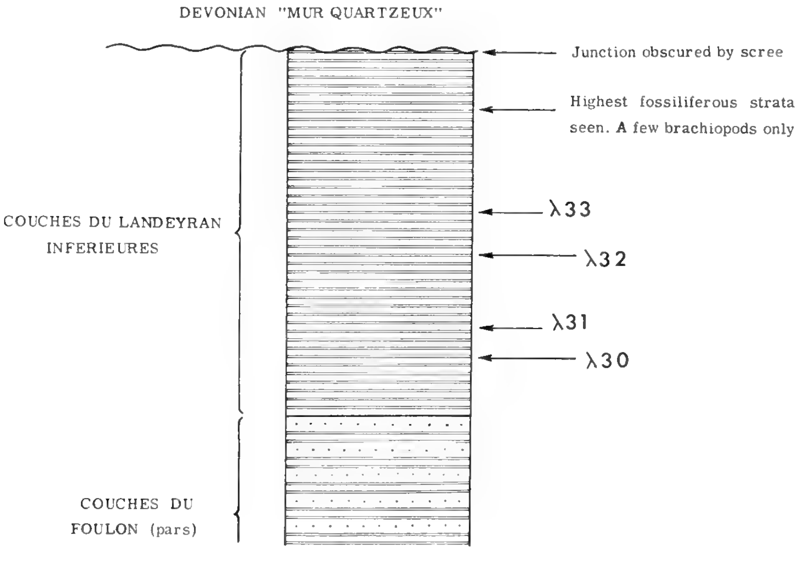

FIG. 7. Succession of the highest Ordovician strata the Devonian unconformity south-west of Le Foulon, showing the stratigraphical position of the principal fossil localities. Vertical Scale, 1 cm. = 10 m.

A large, new collection of graptolites was obtained from this and nearby localities. Individuals are common but the number of species is small, and amongst them Dr. I. Strachan has identified the following : *Didymograptus* cf. *deflexus* Elles & Wood, *D.* cf. *nanus* Lapworth, *Phyllograptus* cf. *angustifolius* Hall, *Tetragraptus* cf. *reclinatus* Elles & Wood. Dr. Strachan (personal communication) considers that all these graptolites are suggestive of what Monsen (1936) called the *Phyllograptus densus* Zone, that is to say, part of the *Didymograptus extensus* Zone of the Arenig Series, according to the more usual convention of Ordovician zoning, though he warns against too detailed correlation over such a large distance and prefers to use here only the Extensus Zone (undivided). The associated shelly fauna contains mainly trilobites and bivalves, but brachiopods, phyllopods and machaeridians also occur (see faunal list).

The Couches supérieures are exposed for some distance along the road in the direction of St. Nazaire de Ladarez. The rocks are generally strongly cleaved and precise measurements are difficult to make, but a south-easterly dip of 76° was obtained at one point. South-east of the St. Nazaire road at locality λ16, the same strata form a wide outcrop which extends up the hillside towards the Devonian " Mur Quartzeux ". Many fossils were collected from a south-easterly traverse made here and the principal localities are shown in Text-fig. 3. The fauna is fairly uniform throughout, with only relatively small variations. *Hanchungolithus primitivus* ranges through the complete succession, having been collected only a few metres below the " Mur Quartzeux ", the actual Ordovician/Devonian junction being obscured by scree. Although lacking at a few points, *Colpocoryphe thorali* extends into the highest Couches du Landeyran, but *Ormathops borni* is known only from the lowest portion (perhaps 85 metres) of the Couches supérieures.

The most fossiliferous outcrops found are those in the south of the Landeyran Valley, where the strata are less disturbed tectonically, but the presence of uncommon specimens of *Hanchungolithus primitivus* enables the Couches supérieures to be traced along the south-eastern side of the valley. The most northerly fossiliferous exposures were found at and near λ8 (see Text-fig. 3). Thence the outcrop narrows north-eastwards below the Devonian unconformity and is judged to terminate along the hill slope to the south-east of the track known as Chemin des Gravénas (see Text-fig. 3). As already stated, the vineyards in the area north of the track are underlain by the Couches du Landeyran inférieures.

The southern extension of the Couches supérieures is limited, and the rocks are absent from the sections near Le Foulon. Accurate mapping is difficult owing to lack of exposures, but a single poorly-preserved specimen of *Hanchungolithus primitivus* found loose on the hillside south-east of l'Escougoussou suggests that the outcrop ends nearby, as the Couches inférieures exposed in the road-section by the farm strike south-westwards towards the adjacent base of the Devonian rocks, only some 150 metres distant. The specimen is preserved in a more compacted, splintery matrix than is found in the sections north of Pont des Quatre Chemins.

The folding of the Couches du Landeyran below the unconformable Devonian is shown in Text-fig. 8 by means of vertical sections. Outside the Landeyran district

the Couches inférieures and Couches supérieures are known from the Boutoury area, near Cabrières, whilst species common to the St. Chinian district and the neighbourhood of the Landeyran Valley and Le Foulon suggest a westwards extension of at least the lower subdivision. However, some facies change might be expected near St. Chinian as the earlier Grès à Lingules do not occur there, nor have any species of the Couches du Landeyran supérieures been found.

The second edition of the 1 : 80 000 Bédarieux Sheet of the Carte géologique de la France (see Blayac *et al.* 1938) gives an over-simplified picture of the Ordovician stratigraphy of the Landeyran Valley–Le Foulon district. It shows the Grès à Lingules of Serrelongue as being followed by two successive groups of strata. The lower of these is indicated as forming the whole of the outcrop between the River Orb and the Devonian " Mur Quartzeux " to the south-west of Le Foulon. The same strata reappear to the north-east, occupy the area between l'Escougoussou and Pont des Quatre Chemins, and then form a nearly parallel-sided outcrop along the western bank of the River Landeyran as far as the Upper Bridge. The outcrop of the higher series of strata is indicated as beginning near Pont des Quatre Chemins and continuing north-eastwards without structural complications, terminating at the Devonian outcrop by the Upper Bridge. The higher strata may be regarded as approximately equivalent to the Couches du Landeyran supérieures and their outcrop should, in fact, extend slightly farther south-westwards towards l'Escougoussou, and terminate in a north-easterly direction before reaching the Upper Bridge. The lower series approximates to the Couches du Foulon plus the Couches du Landeyran inférieures, the structural relationships of which are far from simple at the northern end of the Landeyran Valley.

To summarize, the entire Ordovician succession in the vicinity of the Landeyran Valley may be assigned to the *Didymograptus extensus* Zone of the Arenig Series. The lowest strata, the graptolitic Schistes de Setso, constitute a restricted development and may be represented elsewhere by Thoral's *Taihungshania* [*Miquelina*] *miqueli* Zone. Likewise, the Grès à Lingules probably pass into mudstones to the west and are unknown farther east. Of the Couches du Landeyran, the Couches inférieures contain a distinctive fauna found also at Boutoury and probably also in North Africa, whilst the Couches supérieures are found in a syncline preserved beneath the unconformable Devonian strata of the Landeyran Valley. Their fauna, characterized by *Hanchungolithus primitivus*, occurs also at Boutoury but is unknown elsewhere.

III. FAUNAL LISTS

All the species collected are listed alphabetically within Classes, and in numbered columns denoting stratigraphical subdivisions as follows: 1, Schistes de Setso; 2, Grès à Lingules; 3, Couches du Foulon; 4, Couches du Landeyran inférieures; 5, Couches du Landeyran supérieures. Several brachiopods were found but are excluded from the present lists as they are to form the subject of a separate study by Prof. A. Williams.

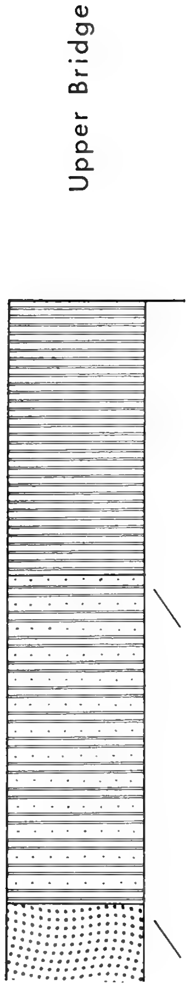

FIG. 8. Diagram
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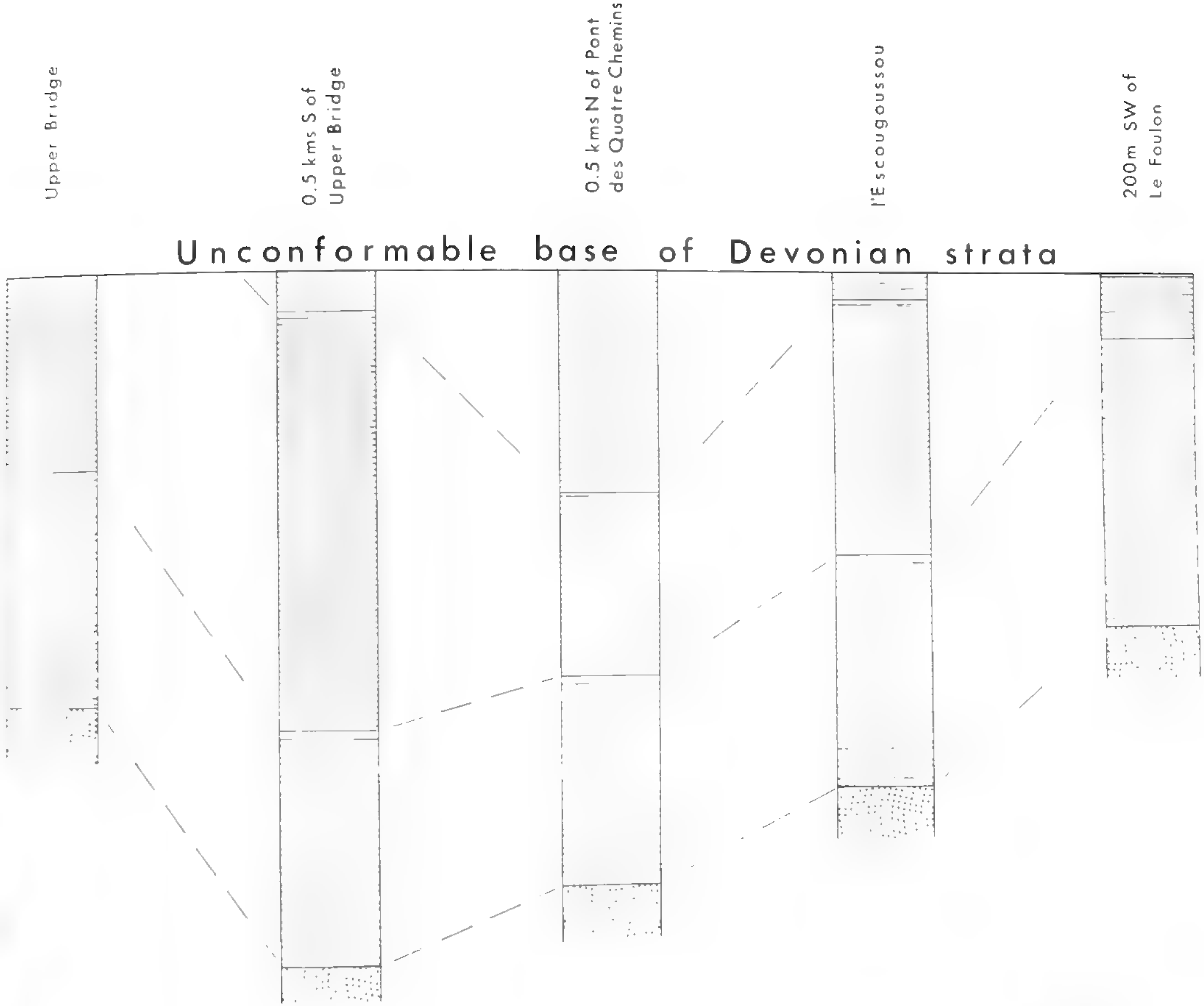

Fig. 8. Diagram illustrating the correlation of the higher Arenig rocks at various points between the northern end of the Landeyran V[illegible] and the Orb Valley near Lugné. The base of the Devonian provides a convenient datum line. For key, see Text-fig. 2. Vertical Scale, [illegible]

	1	2	3	4	5
Hyolithida					
Hyolithes (s.l.) sp.	—	—	—	×	×
Graptolithina					
Didymograptus deflexus Elles & Wood	—	—	—	—	×
D. cf. *deflexus* Elles & Wood	×	—	—	—	×
D. cf. *minutus* Törnquist	—	—	—	×	—
D. cf. *nanus* Lapworth	—	—	—	×	—
D. cf. *protobifidus* Elles	—	—	—	×	—
D. cf. *protoindentus* Monsen	—	—	—	×	—
Didymograptus sp.	—	—	—	×	×
Phyllograptus angustifolius Hall	—	—	—	—	×
Phyllograptus sp.	—	—	—	—	×
Tetragraptus cf. *pendens* Elles?	—	—	—	×	—
T. cf. *reclinatus* Elles & Wood	—	—	—	×	—
T. cf. *serra* (Brongniart)	—	—	—	—	×
Asterozoa					
Chinianaster levyi Thoral	—	—	—	×	—
Machaeridia					
Lepidocoleus sp.	—	—	—	—	×
Plumulites sp.	—	—	—	—	×
Conularida					
Eoconularia? cf. *azaisi* (Thoral)	—	—	—	×	—
Bivalvia					
Babinka prima Barrande?	—	—	—	—	×
Redonia cf. *prisca* Thoral	—	—	—	×	×
cf. *Synek antiquus* Barrande	—	—	—	×	×
Gastropoda					
"*Bellerophon*" cf. *oehlerti* Bergeron	—	—	—	×	×
Lesueurilla cf. *prima* (Barrande)	—	—	—	×	—
Sinuites sp.	—	—	—	—	×
Cephalopoda					
Orthoconic nautiloids indet.	—	—	—	—	×
Phyllopoda?					
Anatifopsis cf. *trapeziiformis* Thoral	—	—	—	—	×
Ribeirella crassa Thoral	—	—	—	—	×
Ribeiria personata Thoral	—	—	—	×	×
R. personata obsoleta Thoral	—	—	—	×	—
Ostracoda					
Primitiid ostracods indet.	—	—	—	×	×

Trilobita	1	2	3	4	5
Ampyx priscus Thoral	—	—	—	×	—
Apatokephalus incisus sp. nov.	—	—	—	×	—
Asaphids indet.	×	—	×	×	×
Basiliella mediterranea sp. nov.	—	—	—	×	×
Basiliella sp.	—	—	—	—	×
Bathycheilus gallicus Dean	—	—	—	×	—
Ceraurinella peregrinus sp. nov.	—	—	—	×	—
Colpocoryphe thorali sp. nov.	—	—	—	×	×
Colpocoryphe sp.	—	—	×	—	—
Geragnostus mediterraneus Howell	—	—	—	×	—
G. occitanus Howell	—	—	—	×	—
Hanchungolithus primitivus (Born)	—	—	—	—	×
Hoekaspis? quadrata sp. nov.	—	—	—	×	—
Megalaspidella (*Megalaspidella*) sp.	—	—	—	×	×
Megistaspis (s.l.) sp.	—	—	—	—	?
Megistaspis (*Ekeraspis*) sp.	—	—	—	×	×
Neseuretus antetristani sp. nov.	—	—	—	—	×
N. arenosus sp. nov.	—	—	×	—	—
N. cf. *arenosus* sp. nov.	—	—	—	×	×
Niobella fourneti (Thoral)	—	—	—	×	—
N. cf. *lignieresi* (Bergeron)	—	—	—	×	—
Niobella? sp.	—	—	—	×	—
Ormathops borni sp. nov.	—	—	—	×	×
Otarion insolitum sp. nov.	—	—	—	—	×
Paramegalaspis cf. *frequens* Thoral	—	—	—	×	×
Paramegalaspis sp.	—	—	×	×	×
Platycoryphe convergens sp. nov.	—	—	—	—	×
Pliomerops escoti (Bergeron)	—	—	—	×	—
Prionocheilus matutinus sp. nov.	—	—	—	×	—
Proetid gen. et sp. indet.	—	—	—	×	—
Selenopeltis binodosus sp. nov.	—	—	—	×	—
Symphysurus sabulosus sp. nov.	—	—	×	—	—
Taihungshania landayranensis (Thoral)	×	—	—	—	—
Taihungshania sp.	—	—	—	—	×

IV. SYSTEMATIC DESCRIPTIONS OF THE TRILOBITES

Family **AGNOSTIDAE** M'Coy 1849

Although Thoral had available a small number of specimens of agnostid trilobites from the Montagne Noire, most of them collected earlier by Miquel, he did not describe them and the material formed the subject of a paper by Howell (1935). In this publication specimens of Middle Cambrian, Tremadoc and Arenig age were described, but only the Arenig forms, or at least a majority of them, are reviewed here. They were assigned by Howell (1935 : 231–238) to four genera, *Trinodus*, *Geragnostus*, *Leiagnostus* and *Micragnostus*. The last three names were new, founded on species from countries other than France, and although it is not proposed here to revise these genera, nevertheless the species from the Montagne Noire assigned to them by Howell are all now placed in *Geragnostus*.

The agnostids from the so-called " Schistes à Calymènes " of Le Foulon and Boutoury were kept apart from those of the Arenig Series at Barroubio and near St. Chinian by Howell, who followed Thoral in assuming that two distinct geological horizons were involved. The present researches suggest that most of, if not all, the Arenig agnostids of this region originate from a single series of strata, those now termed the Couches du Landeyran inférieures, or their lateral equivalents. There is only a single record of agnostids (Thoral 1933 : 148) from what are now called the Couches du Landeyran supérieures. This was not subsequently repeated and I have been unable to confirm it, nor are any agnostids to be found in the appropriate collections at Montpellier University. Howell's descriptions were generally brief and his illustrations suggest an undue amount of " splitting " into species. The original material has been examined in conjunction with my new collections, and as a result I consider that all Howell's species of *Geragnostus*, together with *Leiagnostus foulonensis* Howell and *Micragnostus languedocensis* Howell, may be grouped into no more than two, somewhat variable species of *Geragnostus*.

Genus ***GERAGNOSTUS*** Howell 1935

1939. *Geragnostella* Kobayashi : 167.

In recent years Whittard (1955 : 7) has maintained *Geragnostella* as a separate genus on the basis of the subtriangular cephalon and glabella, the form of the pygidium, and details of the axial region. The genus was founded by Kobayashi (1939 : 167) as a subgenus of *Geragnostus*, using as type-species *Agnostus tullbergi* Novák (1883 : 59, pl. 9, figs. 7–10), described first from the Šárka Beds (Llanvirn Series) of Osek, near Rokycany, Bohemia. A cast of specimens from the same horizon at Šárka, near Prague, figured in manuscript by Novák, is figured here for comparison (Pl. 2, figs. 4, 9). It shows that the tip of the pygidial axis is circumscribed, even though only faintly, by the posterior continuation of the axial furrows, and thus cannot be said to differ significantly from the axis in *Geragnostus*. There is also a very small median tubercle, the same as that called a terminal node by Palmer (1955, text-fig. 1), near the axial tip in *Agnostus tullbergi*, but this is not considered to be of great systematic significance. The cephalon of *Agnostus tullbergi* is indistinguishable from that of a typical *Geragnostus*, and in view of the variability now known to occur within the latter genus I prefer to regard *Geragnostella* as a junior subjective synonym of *Geragnostus*.

In discussing the agnostids from the Montagne Noire, Howell (1935 : 231, 233) erected two separate families, Geragnostidae and Trinodidae, but later recognized their equivalence (*in* Moore 1959 : O 176). The difficulties of distinguishing between *Geragnostus* and *Trinodus* have been discussed by both Ross (1958 : 563–564) and Whittington (1963 : 28). The type-species of *Trinodus*, *T. agnostiformis* M'Coy (1846, pl. 4, fig. 3) from the Ordovician (undifferentiated) of Greenville, Co. Wexford, Eire, was redescribed by Whittington (1950 : 533, pl. 68, figs. 1–3). Unfortunately the thorax and pygidium of *T. agnostiformis* are still not known, and it is therefore impossible to define the genus satisfactorily until they have been described. Never-

theless, various species in which the cephalon generally resembles that of *T. agnostiformis* have been assigned to *Trinodus*, for example *T. tardus* (Barrande) figured by Whittington (1950, pl. 68, figs. 4–6), although such identifications must necessarily assume certain facts which are not yet known. The species attributed to *Trinodus* have in common a relatively short pygidial axis which narrows backwards to a rounded tip, is defined by a continuous furrow, and carries a pair of small antero-lateral lobes together with a median tubercle followed immediately by a transverse furrow. Further research may show these features to be insufficient to maintain *Trinodus* and *Geragnostus* as separate genera, in which case *Trinodus* would take precedence.

Girvanagnostus was erected by Kobayashi (1939 : 166, 167, 174, plate) who listed it variously as a subgenus of both *Trinodus* and *Geragnostus*. Howell (*in* Moore 1959 : O 177) has given *Girvanagnostus* full generic status even though Whittard (1955 : 7) had earlier cast doubt on its validity. The Gray Collection at the British Museum (Natural History) contains numerous specimens of the type species, first described as *Agnostus girvanensis* Reed (1903 : 4, pl. 1, figs. 2–4) ; they include the original of Reed's pl. 1, fig. 2, which is here chosen as lectotype, specimen number In.20609. The radial furrows shown in Reed's reconstruction of the cephalon and pygidium are imaginary, founded only on accidents of preservation, and the species is otherwise indistinguishable from *Trinodus*.

Geragnostus occitanus Howell

(Pl. 1, figs. 1–12 ; Pl. 2, figs. 1–3, 7)

1935. *Geragnostus occitanus* Howell: 231, pl. 23, figs. 4, 5.
1935. *Leiagnostus foulonensis* Howell : 236, pl. 23, figs. 17, 18.
1935. *Geragnostus languidus* Howell : 237, pl. 23, figs. 19–21.
1935 .*Geragnostus boutouryensis* Howell : 237, pl. 23, figs. 22, 23.

Localities and horizon. In the Landeyran Valley–Le Foulon district *Geragnostus occitanus* has been found only in the Couches du Landeyran inférieures, as, in fact, have all other agnostids collected. Localities λ2 and λ5, both near the northern end of the Landeyran Valley, have yielded mainly this species, which has also been found to range through virtually all the succession exposed in the hillside section 250 metres south-west of Le Foulon. Locality λ32 proved particularly rich, and an interesting feature of the strata near Le Foulon is the large proportion of entire dorsal exoskeletons preserved, indicating relatively quiet conditions of deposition.

Figured material. Brit. Mus. (Nat. Hist.) In.57417 (Pl. 2, fig. 7) ; In.57418 (Pl. 2, fig. 1) ; In.57419 (Pl. 2, figs. 2, 3) ; It.140 (Pl. 1, fig. 1) ; It.141 (Pl. 1, fig. 2) ; It.142 (Pl. 1, fig. 3) ; It.143 (Pl. 1, fig. 4) ; It.144 (Pl. 1, figs. 5, 9) ; It.145 (Pl. 1, fig. 6) ; It.146 (Pl. 1, figs. 7, 12) ; It.147 (Pl. 1, figs. 8, 11) ; It.148 (Pl. 1, fig. 10).

Description. The entire dorsal exoskeleton is approximately, or slightly more than, half as broad as long, though all the specimens examined have been affected

to at least a slight degree by dorsal compression. The cephalon is basically subquadrate in plan, the median length being slightly less than the maximum breadth, measured across the mid-point. The frontal and lateral margins of the cephalon are broadly rounded, uniting at anterolateral angles which are also rounded, though with a smaller radius of curvature. The glabellar outline is elongated, semi-elliptical in plan, the basal breadth about two-thirds of the median length. It is circumscribed by a continuous furrow, representing the conjoined axial and preglabellar furrows, which varies in its degree of definition. Sometimes it becomes almost obsolete, particularly frontally, and is generally slightly broader and deeper on internal moulds. At its posterolateral extremities the glabellar outline extends opposite the mid-points of a pair of occipital lobes, each an obtuse triangle in plan with apex directed forwards. These lobes would have been called " basal glabellar lobes " using the terminology of Palmer (1955, fig. 1), but Whittington (1963 : 28) suggests that they are more suitably termed occipital lobes, and his convention is followed here. The occipital lobes are separated by a small, node-like structure which is generally obscured by crushing ; it corresponds to the "median band of the occipital ring " illustrated by Whittington (1963). Immediately outside each occipital lobe is a short (*tr.*), narrow (*exsag.*) posterior border, defined by a furrow which is generally well developed but may be shallow. The border is transversely straight as far as the fulcrum where it expands suddenly to form a short, bluntly-pointed, fixigenal spine (see especially Pl. 1, fig. 9). The glabella carries a small median tubercle at a point slightly in front of centre and immediately behind the apex of a chevron-shaped furrow which is faintly impressed and broadly divergent forwards. Both the furrow and the median tubercle may become almost obsolete, and some specimens show a slight indentation of the lateral margins of the glabella opposite the median tubercle.

The thorax consists of two dissimilar segments of almost equal size, and the descriptive terminology used here is that of Whittington (1963 : 29, fig. 3). The first segment is subrectangular in plan, the length (*sag.*) about a quarter of the breadth (*tr.*), this, in turn, being slightly less than the distance between the lateral border furrows of the cephalon. Most of the segment is occupied by the axial ring, the pleurae being reduced to narrow (*tr.*) strips, their abaxial margins indented at the outer ends of pleural furrows which divide the pleurae into two bands, both of them slightly swollen and the anterior band noticeably the larger. The anterior third of the axial ring is flattened and set lower than the remaining two-thirds, which is divided into three lobes by deep, broad furrows. The median lobe is slightly larger than the lateral lobes and trapezoidal in plan, the sides converging forwards strongly from a posterior margin which occupies about one-third of the breadth (*tr.*) of the segment. The lateral lobes are lozenge-shaped with their long axes converging forwards. The second thoracic segment is shorter (*sag.*) and broader (*tr.*) than the first segment, with an axial ring of similar size and form preceded by a well-developed articulating half-ring. The pleural lobes curve forwards and end in blunt points beyond the pleural tips of the first segment. On each pleura a pleural furrow curves

forwards to the tip and separates a narrow (*exsag.*) anterior band from a posterior band approximately twice as broad.

The pygidium is slightly smaller than the cephalon, the median length more than three-quarters of the maximum breadth, and moderately convex both longitudinally and transversely. The axis occupies about half the frontal projected breadth of the pygidium and more than two-thirds its projected length in, presumably, adult specimens. The sides of the axis converge backwards at about 40° over the anterior two-fifths of their length, but then become less convergent towards the rounded axial tip. Owing to diminution of the furrow defining it, the tip of the axis is sometimes almost indiscernible. The break in continuity of the sides of the axis coincides with a transverse furrow which is sometimes moderately impressed but is more often almost obsolete. Between this furrow and the front of the pygidium the median quarter of the axis is occupied by a raised, longitudinal rectangular structure, the hindmost part of which expands dorsally to form a median tubercle. The frontal two-fifths of the " rectangular structure " are a little broader and coincide with a pair of anterolateral lobes which are delimited posteriorly by a transverse furrow which, like the one behind it, may be moderately impressed or almost obsolete. The pleural lobes are gently convex, decline laterally at about 45° though less so posteriorly, and each has a projected breadth about half that of the axis. The anterior end of each pleural lobe is marked by a narrow (*exsag.*) anterior border, the hindmost part of which is ridge-like, standing higher than the pleural lobe and lateral border, and meeting the latter at an obtuse angle. A deep, narrow (*exsag.*) furrow, continuous with the lateral border furrow, separates the anterior border from the rest of the pleural lobe. The foremost part of the anterior border is declined steeply forwards to form a large articulating facet, running outwards and slightly back. The function of similar facets during enrollment has been demonstrated for *Geragnostus clusus* by Whittington (1963, fig. 3) and is also found in *G. tullbergi* (Novák) (see Pl. 2, fig. 10). The pygidial border broadens a little posterolaterally, where one may find traces of a pair of small, backwardly-directed marginal spines sited approximately in-line with the axial tip.

An interesting feature emerging from the present sample of *Geragnostus occitanus* is the large amount of variation encountered. North American specimens of the same genus were shown by Whittington (1963 : 30) to have the axial furrows of both cephalon and pygidium deeper and broader on internal moulds, owing to folding of the normal thickness of the test, and similar features have been found in the French specimens. In addition, the degree to which the axial furrows, transverse glabellar furrow, median tubercles and pygidial ring furrows are developed, even on the external mould, varies considerably, and one may find gradations between forms in which furrows and tubercles are well defined, and others in which the corresponding features are almost obsolete. This variation does not appear to be dependent on the stage of development attained, and supposedly immature individuals may show obsolete furrows like those of adults. The smallest specimens are, however, characterized by broader cephalic and pygidial borders, as well as by a rather more rectangular pygidial outline.

DISCUSSION. This will be found on p. 278, after the description of *Geragnostus mediterraneus*.

Geragnostus mediterraneus Howell

(Pl. 2, figs. 5, 6, 8)

1935. *Geragnostus callavei* (Raw) var. *mediterraneus* Howell : 231, pl. 23, figs. 6, 7.
1935. *Geragnostus pusio* Howell : 232, pl. 23, fig. 8.
1935. *Micragnostus languedocensis* Howell : 233, pl. 23, fig. 10.
1935. *Geragnostus manifestus* Howell : 238, pl. 23, figs. 24, 25.

FIGURED SPECIMEN. Brit. Mus. (Nat. Hist.) In.57420 (Pl. 2, figs. 5, 6, 8).

LOCALITY AND HORIZON. The only undoubted example of *Geragnostus mediterraneus* found during the present field-work was obtained from the Couches du Landeyran inférieures at locality λ2, in the north-western bank of the river near the northern end of the Landeyran Valley.

DESCRIPTION. For all practical purposes the cephalon of *G. mediterraneus* may be regarded as being indistinguishable from that of *Geragnostus occitanus*, and the single pygidium of *G. mediterraneus* from the Landeyran Valley was found in association with several cephala and pygidia, all of which could be assigned to *G. occitanus*, as interpreted from the type material of that species. The same may also be said of the thorax.

The pygidial outline is transversely straight frontally, and well rounded posteriorly, the frontal breadth about five-sixths of the median length (excluding the articulating half-ring). It is circumscribed by a raised border of variable breadth which is separated from the remainder of the pygidium by a shallow, concentric border furrow. The margin is produced posterolaterally to form a pair of short, backwardly-directed spines, the bases of which are sited opposite the tip of the pygidial axis. The latter is large, occupying frontally almost half the maximum pygidial breadth, with a length almost three-quarters that of the pygidium. It is moderately convex both longitudinally and transversely, and the dorsal surface is almost level over the anterior two-thirds of its length, after which it declines to the axial tip. The outline of the axis narrows a little medially, opposite the second segment, giving a waist-like appearance. The axial tip is broadly rounded in plan, dorsally convex, and the whole axis is delimited by a continuous, uniformly deep furrow. The anterolateral corners of the axis show the development of a pair of small lobes, transversely elongated and subtriangular in plan. Each lobe occupies just over one-third of the frontal breadth of the axis and between one-fifth and one-sixth of its median length. Immediately behind this pair of lobes the axis is crossed by a transverse segment of length slightly greater than that of the anterolateral lobes, delimited by a shallow, transverse furrow and carrying a well-developed, slightly elongated (*sag.*), median tubercle. The tubercle is best developed in the second segment of the axis, behind which it is abruptly truncated, but frontally it dies away more gradually, opposite the anterolateral lobes.

DISCUSSION. In addition to the holotype of *Leiagnostus foulonensis* Howell, a species now placed in the synonymy of *Geragnostus occitanus*, there are, in the collections of the University of Montpellier, two paratypes which deserve mention. One of these, in the Blayac Collection and numbered H.63, is not a trilobite but comprises two small, conjoined valves of the bivalve *Redonia*, bearing a superficial resemblance to the cephalon and pygidium of an agnostid trilobite. The sample numbered H.64 in the Guiraud Collection contains three specimens labelled *a.* (two specimens) and *b.* Of these *b.* is a paratype of *Geragnostus boutouryensis* Howell (now *Geragnostus occitanus*) whilst *a.* is said to be a paratype of *Leiagnostus foulonensis*. One of the two specimens labelled *a.* is too poorly preserved to be certain of its trilobite affinities, whilst the other contains no trilobites, but exhibits the poorly-preserved remains of several small bivalves, possible immature *Redonia*. Two of the valves lie in juxtaposition and, again, simulate an agnostid trilobite, as in the case of paratype H.63. The holotype of *Micragnostus languedocensis* Howell, also in the University of Montpellier, is a very small pygidium, so abraded that it can scarcely be considered identifiable. Judging from the form of the axis, however, it seems probably that the species is founded on an immature specimen of *Geragnostus mediterraneus*. The same may be said for the aptly-named *Geragnostus pusio*, erected on a single, immature pygidium.

Geragnostus mediterraneus was erected by Howell as a variety of *G. callavei* (Raw), but is regarded here as a separate species. *G. callavei* was first described, as *Agnostus callavei* (Raw *in* Lake 1906 : 25, pl. 2, fig. 20), from the Shineton Shales (Tremadoc Series) of Shropshire and may be distinguished by its narrower, less tumid, more parallel-sided pygidial axis in which the posterior segment is slightly longer and notably less expanded than that of *G. mediterraneus*. In addition, the glabella of the Shineton species is parallel-sided over most of its length and relatively broad frontally, contrasting with the almost subtriangular glabella of *G. mediterraneus*.

Kobayashi (1937 : 463) drew attention to what he claimed as a gradual reduction in the surface relief of the exoskeleton in *Geragnostus occitanus*, *G. boutouryensis* and *G. languidus*. Although not specifically stated, his text implies that he believed these to be successive morphological changes, and he had probably been misled by the allegedly later horizon of the two latter species. He also noted " remarkable flanges " (presumably broad pygidial borders) on the pygidia of *G. boutouryensis* and *G. languidus*, features which are present on smaller individuals and are exaggerated by dorsal compression.

The cephalon of *Geragnostus hirundo* Hicks sp. (1875 : 176 ; see also Whittard, 1955 : 7) from the, probably, upper Arenig Series of the Shelve Inlier and South Wales bears an overall similarity to those of *G. occitanus* and *G. mediterraneus* but has a better defined glabella with a deep, transverse furrow and no median tubercle. The pygidial axis resembles that of *G. mediterraneus* in having an expanded posterior segment but is relatively shorter whilst the pygidial border is broader. *Geragnostus caducus* Barrande sp. (1872 : 142 ; see also Whittard 1955 : 8) from the Llanvirn Series of the Shelve Inlier and Bohemia has a cephalon which, according to Whittard, is distinguishable from that of *G. mediterraneus* only by its having a second glabellar

furrow. The pygidium of *G. caducus* has not been described from the type area but Whittard (1955 : 9) has noted a Shropshire specimen as showing some resemblances to that of *G. hirundo*.

Geragnostus fritschi Holub (1908 : 9, pl. 2, fig. 1), from the Šárka Beds (Llanvirn Series) of Osek, Bohemia, has a well-defined pygidial axis rather like that of *G. mediterraneus*, though with a less expanded posterior segment, whilst its glabella is less tapered than that of the French species and has two deep, transverse furrows. Another species from the Šárka Beds, *G. tullbergi* (Novák) has already been discussed and some of the more obvious differences noted.

Several species of *Geragnostus* have been described or redescribed from the Lower Ordovician of Sweden by Tjernvik (1956). *Geragnostus sidenbladhi* (Linnarsson), the type species of the genus, from the late Tremadoc Series, has a pygidial axis and glabella which are much more parallel-sided than those of any species in the Montagne Noire (Tjernvik 1956 : 188). *G. wimani* Tjernvik (1956 : 192) from the early Arenig Series closely resembles *G. occitanus* in several respects and the cephala are almost identical, but the anterior half of the pygidial axis of the Swedish species is more strongly convergent, followed by a slightly smaller posterior segment than that of the French form. The apparently broader pygidial border of *G. wimani* may be due to compression. *G. crassus* Tjernvik (1956 : 190), from the later Tremadoc and early Arenig Series, has a cephalon generally similar to that of *G. occitanus* and *G. mediterraneus*, though with a broader border. The pygidium of *G. crassus* is very like that of the latter species in having a large posterior axial segment, but the axis is slightly broader and more parallel-sided than that of *G. mediterraneus*.

Family **RAPHIOPHORIDAE** Angelin 1854

Genus ***AMPYX*** Dalman 1827

Ampyx priscus Thoral

(Pl. 3, figs. 1–9 ; Pl. 4, figs. 1–6)

1935*a*. *Ampyx priscus* Thoral : 305, pl. 28, figs. 7–10, pl. 30, fig. 6.
1946. *Ampyx priscus* Thoral ; Thoral : 92.

LECTOTYPE, here chosen. The cranidium figured by Thoral 1935*a*, pl. 28, fig. 9. A cast of this specimen is now illustrated (Pl. 3, figs. 3, 4, 9).

FIGURED MATERIAL. Brit. Mus. (Nat. Hist.) I.15880 (Pl. 3, fig. 6) ; It.150 (Pl. 3, figs. 1, 7 ; Pl. 4, fig. 1) ; It.151 (Pl. 4, fig. 2) ; It.152 (Pl. 4, fig. 3) ; It.153 (Pl. 4, fig. 4) ; It.154 (Pl. 4, fig. 5) ; It.155 (Pl. 4, fig. 6) ; also specimens in the University of Montpellier, including Pl. 3, fig. 5, and a cast (Pl. 3, figs. 2, 8) of a paralectotype pygidium figured by Thoral (1935*a*, pl. 28, fig. 10).

LOCALITIES AND HORIZONS. All the specimens of *Ampyx priscus* collected from the Landeyran Valley–Le Foulon district during the present field-work were obtained from the Couches du Landeyran inférieures. Most were collected from $\lambda 32$ at the hillside section 240 metres south-west of Le Foulon, but the species occurred also at

λ30, 31 and 33. A single specimen (Pl. 3, fig. 6) from an unspecified locality in the Landeyran Valley, collected some years ago by C. Escot and now in the British Museum (Natural History), is probably also from the same horizon, judging by the state of preservation. Several others occur in old collections from the Boutoury district (for example, Pl. 3, fig. 5), probably at the same horizon. The type material came from the St. Chinian district, some 14 kilometres south-west of the Landeyran Valley, so that the lateral equivalents of the Couches du Landeyran inférieures may crop out there, although Thoral (1935*a* : 307) suggested that the species might occur in the Tremadoc Series, at which horizon he claimed to have found it in the Monts de Lacaune.

DISCUSSION. *Ampyx priscus* was founded by Thoral on a number of syntypes, all of which were preserved in siliceous nodules as either internal or external moulds. Although this material had the advantage of being uncrushed, it comprised only disarticulated cranidia and pygidia ; nothing was known of the frontal spine, librigenae and hypostoma, but these have now been found near Le Foulon, though compressed to a greater or lesser degree in shaly mudstones. The glabella, excluding frontal spine, of the lectotype extends a little way in front of the fixigenae, but in specimens from near Le Foulon this feature is variable owing to crushing, so that the glabella may appear to end slightly behind or in front of the fixigenae (see Pls. 3, 4). The frontal spine has not been seen in its entirety, but its length was originally at least one and a half times that of the remainder of the glabella plus the occipital ring. The librigenae are narrow for the most part, broadening a little medially and produced posterolaterally to form a pair of long, curved, librigenal spines. The latter arch outwards and backwards, and their original length was at least four times that of the glabella, excluding frontal spine. They generally resemble the librigenal spines of *Ampyx virginiensis* Cooper (1953 : 16 ; Whittington 1959 : 465).

The hypostoma of *Ampyx priscus* is now known from one incomplete specimen and is almost as broad as long, excluding the anterior wings. The anterior margin arches gently forwards, is separated from the median body by a broad (*sag.*), shallow furrow, and extends laterally towards the incompletely-preserved anterior wings. Behind the last-named, the hypostoma is almost parallel-sided with a narrow, rim-like, lateral border, separated from the subcircular, gently convex median body by a conspicuous lateral border furrow. The posterior margin is convex backwards, well rounded, with a posterior border which is slightly broader (*sag.*) than the lateral border and also bounded by a well-defined furrow. The posterior and lateral borders fuse posterolaterally, the junction of the two being obtusely subangular.

For his description of the thorax of *A. priscus* Thoral (1935*a* : 306) had available a cephalon and pygidium, each with five attached segments, and the number of segments in the complete thorax could not be determined. Most of the new material does not show the thorax clearly but one specimen (Pl. 4, fig. 2), though poorly preserved, suggests that there are six segments, as in other species of *Ampyx*.

The type species of *Ampyx*, *A. nasutus* Dalman (see Whittington 1950 : 554) from the upper Arenig Series of Sweden, has a glabella not unlike that of *A. priscus*,

but it is slightly broader frontally and projects farther forwards in front of the fixigenae, which are smaller and more triangular in plan. The pygidium of the Swedish species is also notably longer. *Ampyx linleyensis* Whittard (1955 : 20) from the lower Llanvirn Series of the Shelve Inlier has more complex glabellar lobation than *A. priscus*, and the fixigenae are narrower frontally. The hypostoma of *A. linleyensis* has been described (Whittard 1955, pl. 2, fig. 8) and differs markedly from that of the French species, having a more ovoid median body, narrowing posteriorly. In addition there are lateral indentations separating a pair of triangular posterior wings from anterior wings which are sited opposite the centre of the median body. The hypostoma of *Ampyx priscus* is closer to that of *A. virginiensis* Cooper (see Whittington 1959 : 468) but is more quadrate in plan and apparently lacks the anterolateral expansions of the American species. The Swedish Arenig species *Ampyx obtusus* Moberg & Segerberg (1906 : 100 ; see also Tjernvik 1956 : 271) has fixigenae closely similar to those of *A. priscus*, but the glabella is slightly shorter and narrower whilst the pygidium is longer and smoother with a more angular margin.

Another raphiophorid described from the Montagne Noire is *Ampyx? villebruni* Thoral (1935*a* : 307), from the Arenig of the St. Chinian district. The species is unusually small and needs to be redescribed, but its affinities appear to lie with such genera as *Ampyxina* and *Orometopus* rather than with *Ampyx*.

Family **TRINUCLEIDAE** Hawle & Corda 1847

Subfamily **HANCHUNGOLITHINAE** Lu 1963

Genus ***HANCHUNGOLITHUS*** Lu 1954

Hanchungolithus primitivus (Born)

(Pl. 5, figs. 1–9)

1921. *Trinucleus primitivus* Born : 191, fig. 1.
1927. *Cryptolithus primitivus* (Born) Stetson : 89, 92.
1935. *Trinucleus primitivus* Born ; Thoral : 175.
1957. *Myttonia primitiva* (Born) Whittard : 267, pl. 1, figs. 1–5.
1963. *Hanchungolithus primitivus* (Born) Lu : 338.
1964. *Hanchungolithus primitivus* (Born) ; Lu : 293.

Figured material. Brit. Mus. (Nat. Hist.) In.56534 (Pl. 5, figs. 2, 5) ; In.56551 (Pl. 5, fig. 1) ; In.57935 (Pl. 5, fig. 4) ; In.57939 (Pl. 5, fig. 7) ; In.58591 (Pl. 5, fig. 3) ; In.58594 (Pl. 5, fig. 9) ; In.58596 (Pl. 5, fig. 6) ; In.58600 (Pl. 5, fig. 8).

Localities and horizons. Born's type material must have been obtained from the roadside exposure in the southern part of the Landeyran Valley denoted here by the symbol $\lambda 17$ (see Text-fig. 3). Although not particularly common at this point the species is much more abundant at numerous other places in the vicinity, and localities $\lambda 19$ and $\lambda 20$ proved especially fruitful. All are in the Couches du Landeyran supérieures, for which subdivision *H. primitivus* is taken as the guide fossil. The best development of these strata is in the southern part of the Landeyran Valley,

and there is an apparent thinning north-eastwards owing to overstep at the base of the succeeding Devonian rocks (see Text-fig. 8). As noted earlier, several specimens housed in old collections at Montpellier University were obtained from the Boutoury district, near Cabrières, some 25 km. east-north-east of the Landeyran Valley.

DISCUSSION. Whittard (1957) has given a detailed description of *H. primitivus* to which little need be added. The thorax is known now to comprise the normal trinucleid complement of six segments, and has been found enrolled with the posterior margin of the pygidium abutting against the inner margin of the ventral lamella of the cephalic fringe. Although Whittard ascribed Born's species to his own genus *Myttonia*, from the early Arenig Series of the Shelve Inlier, I agree with Lu (1963 : 338) that it is better placed in *Hanchungolithus*. The cephalic fringe of *Myttonia confusa*, the type species (see Whittard 1955 : 29, pl. 3, figs. 5–7), carries a large number of pits, randomly arranged and of almost uniform size, and thus contrasts markedly with those of *Hanchungolithus multiseriatus* Endo sp. (see Lu 1957, pl. 155, figs. 5–7 ; 1963 ; 1964) and *H. primitivus*. Both these species have a frontal group of large pits with fairly regular radial and concentric arrangement, of which the outermost concentric row is continued anterolaterally, though composed there of slightly smaller pits, less regularly disposed. The remainder of the fringe is covered with innumerable, very small pits and there is no trace of regular arrangement. *H. primitivus* bears a remarkable resemblance, and is certainly related, to *H. multiseriatus*, but the two can be distinguished and I disagree with Lu's assertion (1964 : 293) that they are probably synonymous. The cephalic fringe of *H. multiseriatus* is broader (*sag.*) frontally than that of *H. primitivus*, and although adult specimens of both species have two concentric rows of large pits, I_1 and I_2, at the sagittal line, in the Chinese species a third concentric row is strongly developed between I_1 and I_2, generally at about R_2 or R_3. The corresponding row of *H. primitivus* does not appear until about R_5 or R_6 and is made up of relatively smaller pits. One of Lu's specimens (1964, pl. 2, fig. 6) shows a number of large pits arranged in four to five concentric rows at least from about R_6 to R_9, but the corresponding features are much less well developed in *H. primitivus*. Judging from the illustrations, the thickened rim of the cephalon is broader and more strongly developed in *H. primitivus*, the alar lobes are more distinct, and the numerous pits covering the greater part of the cephalic fringe are generally smaller and more closely-grouped than those of *H. multiseriatus*. The pygidium is broadly similar in both species, with the side-lobes ornamented by only one or two pairs of furrows. The axis of *H. multiseriatus* is, however, better segmented with three axial rings well defined and another three less so, whilst that of *H. primitivus* has only two clearly marked rings followed by traces of others.

Several immature specimens of *Hanchungolithus primitivus* have been collected, but as they are all disarticulated fragments, mostly cephala or cranidia, it is difficult to assign them to their appropriate stages of development. One of the smallest available is an incomplete cephalon (Pl. 5, fig. 8) with an estimated length and breadth (excluding librigenal spines) of 3·8 mm. and 1·2 mm. respectively. The

margin is thickened, especially anterolaterally, and continues in an unbroken line along the spines, which are stouter and more splayed backwards than in the adult. Alar lobes are well developed, and from the outer end of the short (*tr.*), left ocular ridge runs a single nervure, represented by a thin raised ridge directed towards the genal angle. A similar structure on a much larger individual has been figured by Whittard (1957, pl. 1, fig. 3). This small specimen corresponds in size with Lu's interpretation (1964, pl. 2, fig. 3) of Meraspis Degree 3 in *Hanchungolithus multiseriatus*, but exhibits less mature characters. Several developmental stages were illustrated by Lu (*loc. cit.*) but all lack the associated thorax and pygidium, so there must be some doubt as to their status. A cephalon of *H. primitivus* (Pl. 5, fig. 1) 5·0 mm. wide and 1·9 mm. long has distinct alar lobes 0·5 mm. long, separated by broad alar furrows, and short (*tr.*), transversely straight ocular ridges sited a little in front of centre of the glabella. This specimen is only slightly larger than Meraspis Degree 4 of *H. multiseriatus* as figured by Lu (1964, pl. 2, fig. 4) but has better developed alar lobes and a thicker margin. There seems also to be a smaller development of fringe pits frontally, but this part of the cephalon is difficult to interpret from the published photograph. Another cephalon of similar size (Pl. 5, fig. 6) is relatively longer, with breadth 5·2 mm. and length 2·2 mm., though this may be due to crushing. The thorax of this specimen is slightly disarticulated but, showing four segments, probably represents Meraspis Degree 4, and has a pygidium which is longer and more angular posterolaterally than that of the adult trilobite. Pl. 5, fig. 7 shows a cephalon 6·0 mm. broad and 2·4 mm. long which has swollen, oval alar lobes and noticeably short (*tr.*) ocular ridges directed slightly backwards abaxially. The specimen is slightly larger than the supposed Meraspis Degree 5 of *H. multiseriatus* (see Lu 1964, pl. 2, fig. 5), and differs from the latter in having thicker, less transverse ocular ridges, and considerably more conspicuous alar lobes.

Family **PLIOMERIDAE** Raymond 1913

Subfamily **PLIOMEROPSINAE** Raymond 1913

Genus ***PLIOMEROPS*** Raymond 1905

It was stated by Harrington (*in* Moore 1959 : O 439 *et seq.*) that the cephalon of *Pliomera* differs from that of *Pliomerops* in having an indented frontal glabellar lobe, a denticulated anterior border, a gonatoparian facial suture (as opposed to proparian in *Pliomerops*), and small eyes sited posteriorly rather than medially. In the same publication, however, he departed slightly from this definition by including within *Pliomerops* the Bohemian species *P. senilis* (Barrande), in which the eyes are placed notably far forwards. This last feature also characterizes the only representative of the Pliomeridae found in the Montagne Noire, and it is preferred here to extend the limits of the diagnosis of *Pliomerops* so as to include such forms.

Pliomerops escoti (Bergeron)

(Pl. 6, figs. 1–4, 6, 8–10)

1895. *Amphion escoti* Bergeron : 472, pl. 4, figs. 6–8.
1941. *Amphion escoti* Bergeron ; Thoral : 142, pl. 1, figs. 1–4. Includes full synonymy of the species.

Figured material. Brit. Mus. (Nat. Hist.) I.15877 (Pl. 6, fig. 4) ; I.15878 (Pl. 6, figs. 6, 8, 10) ; It.158 (Pl. 6, figs. 1, 2) ; It.159 (Pl. 6, fig. 3) ; It.161 (Pl. 6, fig. 9).

Localities and horizons. All the specimens collected here are from locality λ2, in the river bank near the northern end of the Landeyran Valley. The rocks form part of the Couches du Landeyran inférieures. The two figured specimens from the Escot Collection (Pl. 6, figs. 4, 6, 8, 10) are not precisely localized within the same valley, but judging from their state of preservation they derive from a similar horizon and, possibly, locality. Bergeron's type material came from near Cabrières, presumably from an horizon at least approximating to that of the Couches du Landeyran inférieures.

Description. The cranidium is almost three times as broad as long. The glabella, with length and breadth about equal, is only gently convex both longitudinally and transversely, though the actual amount may be obscured by slight dorsal compression when preserved in an argillaceous matrix. The glabellar outline is sub-pentagonal, bluntly pointed frontally, the gently curved sides slightly divergent forwards, with minor indentations at the outer ends of the glabellar furrows. There are three pairs of glabellar lobes, delimited by pairs of glabellar furrows which extend inwards on either side for about one-third of the breadth of the glabella, leaving a smooth median band. The third glabellar furrows are moderately impressed, arching inwards and back so as to end opposite the mid-points of the third glabellar lobes. The second and third pairs of furrows are parallel to one another, and the second lobes are similar in size to those of the basal pair. The first glabellar furrows are situated well forwards, just behind the mid-points of the anterolateral margins of the glabella. In consequence the frontal glabellar lobe is very small, at first expanding forwards and then contracting to a blunt point frontally, with maximum breadth less than half that of the glabella. The first glabellar lobes are subpentagonal in plan, their long axes widely divergent forwards and with their pointed apices situated at the intersection of the axial furrows, lateral border furrows and preglabellar furrow. The first glabellar furrows extend inwards a shorter distance than those of the other pairs, though ending longitudinally in-line with them, and become noticeably shallower over their length (*tr.*), unlike the other glabellar furrows which are of more even depth. The anterior border is of uniform breadth (*sag.*), equal to about one-eleventh of the glabellar length (*sag.*), and arched forwards parallel to the front of the glabella. There is no clear differentiation of preglabellar furrow, preglabellar field and anterior border furrow, and the anterior border is separated from the glabella by a uniformly broad furrow, sub-quadrate in cross-section. Overall the axial furrows

are gently convex outwards, converging a little at each glabellar furrow so that the tips of the glabellar lobes are, in turn, slightly convex in plan. The lateral border, though not well known, is well developed and bounded by a strong lateral border furrow. The occipital ring is longest (*sag.*) medially, slightly less than one-fifth the length of the glabella, its posterior margin almost straight but the anterior margin arched forwards, ending laterally in a pair of widely divergent occipital lobes. The pleuroccipital segment is transversely straight and ridge-like as far as the fulcra, coincident with a deep, narrow (*exsag.*), pleuroccipital furrow. Beyond the fulcra the pleuroccipital segment widens (*exsag.*) at first but then narrows to the rounded genal angles, whilst the pleuroccipital furrow becomes broader and shallower, finally curving forwards to join the lateral border furrows. The eyes are sited in a conspicuously forward position, opposite the posterior halves of the first glabellar lobes. The outer margins of the palpebral lobes are almost straight, running outwards and backwards at about 45° so that the visual surfaces, which have not been found preserved, must have faced anterolaterally. The posterior halves of the palpebral lobes are thickened slightly and the lobes themselves are defined by sharply incised palpebral furrows, the hindmost parts of which turn outwards and die out. Frontally the palpebral furrows end a short distance from the lateral border furrows, but the posterior edges of the latter furrows are reached by the forward continuation of the palpebral lobes as eye-ridges which are then flexed adaxially. The fixigenae are of notably large size, though the foremost portions are conspicuously small between the palpebral lobes and the axial furrows. The anterior branches of the facial suture run sharply inwards from the eyes to cut the lateral border furrows and the outer ends of the anterior border. The posterior parts of the fixigenae are broad (*exsag.*) and the posterior branches of the facial suture are widely and uniformly arched backwards to the genal angles. The surface of most of the cephalic test, excluding furrows, is finely granulated, but that of the fixigenae is pitted.

In his description of the species Thoral (1941 : 145) did not describe or figure the hypostoma which, he said, was incompletely known. A single hypostoma of cheirurid type was found in the Landeyran Valley in association with other known fragments of *Pliomerops escoti*, and in the absence of other more suitable contenders it is provisionally assigned to that species (see Pl. 6, figs. 1, 2). The overall outline is subrectangular, the maximum breadth about three-quarters of the median length, and the entire hypostoma is only gently convex, both longitudinally and transversely. The median lobe is almost oval in plan, its breadth a little less than the length. The median furrow is developed only laterally, the two furrows so formed running adaxially backwards from the lateral border furrows and becoming progressively shallower until they are finally obsolete, leaving the median third of the hypostoma unfurrowed. The length of the median body, as measured from the inner ends of the two parts of the median furrow, is slightly less than two-thirds of the total length of the hypostoma. The anterior border forms a narrow rim, ventrally concave, its margin well rounded in plan and continuing laterally to form the curved anterior margins of the anterior wings. The latter have almost transversely straight posterior margins and are strongly deflected dorsally. The lateral borders are longitudinally straight, more

strongly developed than the anterior border, and arise from immediately outside the outer ends of the median furrow. They are delimited adaxially by furrows, which are deep frontally but become shallow posteriorly, and coalesce with the broad, posterior border furrow. The posterior border forms a rim, broader (*sag.*) and more strongly curved than the anterior border, and its junction with the lateral borders is marked by a pair of small marginal spines, directed backwards abaxially and corresponding in position to posterior wings. The posterior lobe is subcrescentic in outline, arching forwards anterolaterally but confluent over its median third with the anterior lobe. The incompletely preserved external mould shows that at least part of the ventral surface of the median body was covered with thin, raised, anastomosing ridges forming a Bertillon pattern, whilst the lateral borders and posterolateral marginal spines carry thicker terrace lines.

On the basis of material from the Cabrières district it is known that the thorax of *Pliomerops escoti*, like that of *P. senilis* (Barrande), contains only fourteen segments. The axis is relatively narrow, only about one-quarter of the thoracic breadth, and stands slightly higher than the side-lobes. The axial rings are transversely straight over most of their length (*tr.*), but the outer ends form a pair of small axial lobes, directed anterolaterally. Each pleura is flat for about half its length (*tr.*) as far as the fulcrum, but then becomes moderately declined. It is divided into two bands of which the posterior is the larger and more conspicuous, thickened so as to form a prominent ridge. This is uniformly developed as far as the fulcrum but then gradually diminishes as it follows the curved posterior margin of the outer part of the pleura, finally dying out before reaching the pleural tip. There is a trace of a narrow (*exsag.*) posterior flange immediately behind the posterior band. As the posterior band narrows beyond the fulcrum, so the anterior band broadens and is deflected ventrally to form an articulating facet. The pleural tip is bluntly pointed.

The pygidium, excluding the articulating half-ring, has a median length just over two-thirds of the maximum breadth. The axial outline is that of an acute isosceles triangle, equal to about three-quarters of the total pygidial length and with slightly convex sides converging backwards at about 40° to the sharply-pointed tip. There are five well-defined axial rings, separated from one another by deep, broad (*sag.*) ring furrows. The first ring is arched forwards slightly in plan, but the other rings become progressively less so, and the fifth is transversely straight. The terminal piece is conspicuously triangular, and the axial furrows are deep, wide and almost straight. The pleural regions comprise five pairs of pleurae, each ending posterolaterally in a pair of long free points. The first pair of pleurae run outwards and slightly backwards for about one-third of their length (*tr.*) but then flex sharply backwards, continuing as slender free points and diverging at about 40°. The remaining pairs of pleurae become progressively less flexed but more strongly directed backwards, until the hindmost pair run parallel to each other and extend beyond the tip of the axis.

A single specimen of a transitory pygidium (see Pl. 6, fig. 9) was collected in the Landeyran Valley. Six axial rings and pleurae are present, and presumably Meraspis Degree 13, is represented. The pygidium differs also from that of a typical holaspis

in being slightly broader, and in having an axis with a less triangular outline, and the free points of the pleurae directed less strongly backwards.

DISCUSSION. Specimens of *Pliomerops escoti* from the Montagne Noire have often been referred to *Pliomerops* [*Amphion*] *lindaueri* Barrande sp. (1852 : 820, pl. 30, figs. 12, 13). The latter species was described from only a single pygidium, preserved as an internal mould and now in the National Museum, Prague (number ČD. 142). Dr. R. Horný kindly informs me that the specimen is from the Arenig Series at Komárov, Bohemia, a locality now no longer available. Judging from the holotype, *Pliomerops lindaueri* is probably a larger species than *P. escoti*, but the two are of generally similar type, at least as far as the pygidium is concerned. However, the pygidial pleurae and pleural spines are turned backwards more sharply in *P. escoti*, so that the line of maximum pygidial breadth is sited farther back than in *P. lindaueri*. Thoral's comparison (1941 : 146) of the cephalon of *P. escoti* with that of *P. lindaueri* must be disregarded as the latter has yet to be described.

Pliomerops escoti differs in several respects from the type species of the genus, *P. canadensis* (Billings), which has been discussed and refigured by both Cooper (1953 : 26) and Whittington (1961 : 917). The second and third glabellar furrows of *P. escoti* curve backwards more strongly, the third glabellar lobes are larger, and, as noted earlier, the eyes are sited close to the glabella and well forwards, opposite the posterior half of the first glabellar lobes. This last contrasts sharply with the position of the eyes in *P. canadensis*, about midway between the axial furrows and the cephalic margin, and opposite the posterior half of the second glabellar lobes. The hypostoma of *P. canadensis* (see Whittington 1961, text-fig. 2C, pl. 101, fig. 19), roughly ovoid in plan with broad, continuous lateral and posterior borders, is quite unlike that tentatively assigned to *P. escoti*.

The species most obviously related to *Pliomerops escoti* is *P. senilis* (Barrande 1872 : 118) from the Šárka Beds (Llanvirn Series) of Osek, Bohemia, which is generally similar and shares with it the unusually anterior position of the eyes. *P. senilis* is a large species, probably larger than *P. escoti*, with straighter, more divergent axial furrows and smaller third glabellar lobes, whilst the palpebral lobes run more strongly backwards abaxially. The hypostoma of *P. senilis* differs from that assigned to *P. escoti* by being divided into two subequal parts by the median furrow, having a broader border, and lacking the spinose posterior wings of the French species. The two pygidia are superficially similar but that of *P. escoti* has a narrower axis and slimmer pleurae which flex backwards more strongly.

Family **CHEIRURIDAE** Salter 1864

Subfamily **CHEIRURINAE** Salter 1864

Genus ***CERAURINELLA*** Cooper 1953

Ceraurinella peregrinus sp. nov.

(Pl. 6, figs. 5, 7 ; Pl. 7, figs. 1–9)

DIAGNOSIS. *Ceraurinella* with glabella well rounded frontally and almost parallel-sided. Three pairs nearly equidimensional glabellar lobes present ; basal pair

delimited by basal glabellar furrows which become shallower posteriorly to occipital furrow. Anterior border narrow (*sag.*), steeply upturned. Eyes opposite second glabellar furrows. Glabellar surface granulated, that of fixigenae pitted. Genal angles forming short fixigenal spines. Thorax of eleven segments, ending laterally in long, free spines. Posterior margin of pygidium with three pairs unequal spines which become progressively shorter from first to third, those of first pair conspicuously larger than others.

HOLOTYPE. Guiraud Coll., University of Montpellier (Pl. 7, figs. 1–3, 6, 7).

PARATYPES. Guiraud Coll., University of Montpellier (Pl. 7, fig. 4 and Pl. 7, figs. 8, 9); Brit. Mus. (Nat. Hist.) It.160 (Pl. 7, fig. 5); It.169 (Pl. 6, figs. 5, 7).

LOCALITIES AND HORIZON. The material at Montpellier University is stated to be from " Le Foulon ", and its state of preservation matches that of the strata at the hillside section about 250 metres south-west of Le Foulon. Specimen It.169 is from $\lambda 32$ at the same section, whilst It.160 is from $\lambda 2$ near the northern end of the Landeyran Valley. In all cases the horizon either is, or is presumed to be, in the Couches du Landeyran inférieures.

DESCRIPTION. The cranidium has been found reasonably preserved in only two small specimens, one from the northern end of the Landeyran Valley and the other from the area south-west of Le Foulon. Both are incomplete and slightly damaged but, as far as can be judged, the glabella is moderately convex, slightly longer than broad, almost parallelsided, narrowing a little from the occipital furrow to just behind the first glabellar furrows, and well-rounded frontally. There are three pairs of glabellar lobes, almost equal in size and each about one-quarter of the glabellar length. Those of the third pair approach the " cat's ear " outline, each being generally subcircular with an angular projection directed anterolaterally towards the axial furrow. Their distal margins are slightly convex beyond the otherwise straight sides of the glabella. The third glabellar furrows are deep, running inwards and moderately backwards from the axial furrows for three-quarters of the breadth of the basal lobes and then turning through about 60° so as to run almost straight backwards to the occipital furrow, at the same time becoming markedly shallower. The second glabellar lobes are subrectangular in plan, slightly longer (*tr.*) than those of the first pair and occupying about one-third the glabellar breadth. The second glabellar furrows run inwards and slightly backwards from the axial furrows, curving gently and becoming a little shallower towards their inner ends. The first glabellar furrows are similar to the second furrows, though perhaps a little shorter (*tr.*) as far as can be seen, and the first and second glabellar lobes are of approximately similar size. The frontal glabellar lobe is semi-elliptical in plan, three times as broad as long, broadly convex frontally and curving smoothly backwards to the first glabellar furrows, the anterolateral angles of the glabella being well rounded. The axial furrows are almost straight overall with only a slight outward curvature posteriorly to accommodate the third glabellar lobes. Frontally they are continuous with the deep, narrow, preglabellar furrow circumscribing the frontal glabellar lobe. The anterior border forms a narrow (*sag.*), steeply upturned brim running subparallel

to the front of the glabella, from which it is separated by a deep furrow. The last-named widens (*exsag.*) a little abaxially towards its junction with the axial furrows opposite the first glabellar furrows. The upper part of the anterior border is slightly thickened so that it appears superficially to be separated from the glabella by a narrow (*sag.*) preglabellar field, but no anterior border furrow is developed. The furrow separating the anterior border and the frontal glabellar lobe continues laterally beyond the axial furrows so as to form a deep depression between the ends of the anterior border and the narrow, declined, frontal portions of the fixigenae, and opposite the outer ends of the first glabellar furrows. The occipital ring and furrow, though incompletely preserved, appear to be transversely straight medially, and curve forwards slightly at their outer ends, where the occipital ring is a little narrower (*exsag.*). The pleuroccipital segment is narrower (*exsag.*) immediately outside the axial furrows but increases uniformly in breadth towards the genal angles which are produced to form a pair of short, stout, fixigenal spines, directed posterolaterally. The pleuroccipital furrow is deep and narrow near the axial furrows but widens noticeably towards the genal angles, where it curves forwards, turning through more than a right angle to join the lateral border furrows. One of the paratypes (Pl. 6, figs. 5, 7) shows a small lateral projection on the left margin of the cephalon just in front of the line of the pleuroccipital furrow, but there is insufficient evidence to show whether a pair of true marginal spines (profixigenal spines of Harrington *in* Moore 1959 : O 53) is present. Owing to crushing, the exact position of the eyes is a little difficult to judge, but they apparently occupy a position opposite the second glabellar furrows, the anterior part of the second glabellar lobes, and probably also the hindmost part of the first glabellar lobes. Only the left palpebral lobe is known, which is narrow, prominent, ridge-like and runs abaxially backwards. There is a deep, narrow, palpebral furrow which widens and dies out to both front and back. The anterior branches of the facial suture are slightly convergent forwards, sub-parallel to the axial furrows. The posterior branches run almost straight outwards from the palpebral lobes as far as the lateral border furrow, where they begin to curve gently back, cutting the lateral margins approximately in-line with the anterior ends of the third glabellar furrows. With the exception of the smooth furrows, the surface of the glabella is covered with fine, evenly-distributed granules, among which are slightly larger, less crowded tubercles. The surfaces of the lateral border, pleuroccipital segment and fixigenae are all finely granulated but the granulation of the fixigenae is accompanied by pitting which is particularly conspicuous postero-laterally. The fine granulation traverses the lateral border furrows but is less well developed there.

The hypostoma is known from a single, indifferently-preserved specimen, an external mould forming part of the holotype. The anterior border is not preserved, but was probably gently convex forwards. The original outline of the hypostoma was semi-elliptical, with the median length about equal to the maximum breadth, excluding the anterior wings which are broken off. The median body is moderately plump and stands a little higher than the lateral borders. In plan it is roughly pear-shaped, narrowing backwards, but owing to crushing it is not clear whether the

posterolateral indentations are, in fact, a primary feature. The posterior border is narrow (*sag.*) medially (probably less than one-sixth of the total original length) and confluent with the lateral borders which are slightly broader, especially frontally, near the conjectured position of the anterior wings. The entire border forms a collar-like structure which declines inwards, particularly anteriorly, and is separated from the median lobe by a broad border furrow. Fine granules cover the surface of the median body and most of the border, but the deepest parts of the border furrow are smooth.

The thorax comprises eleven segments, the axis being moderately convex and standing higher than the side-lobes. The median part of each axial ring is transversely straight but the ends curve forwards slightly so as to form a pair of axial lobes, poorly defined on the external mould but quite distinct, and preceded by a pair of apodemes, on the internal mould. The axis occupies about one-quarter of the thoracic breadth and is separated from the side-lobes by well-defined axial furrows which are slightly indented by the abaxial margins of the axial lobes. The articulating half-rings are well developed, each separated from the axial ring by an articulating furrow which curves slightly forwards medially. From the axial furrows the adaxial portions of the side-lobes are flat as far as the fulcra, beyond which they are slightly declined. In plan view each segment is parallelsided and curves gently back as far as the fulcrum. From the internal mould it is apparent that the thoracic doublure was relatively wide, reflexed ventrally so as to end just outside the line of the fulcrum, the distance from the pleural tip to the inner margin of the doublure being approximately one-fifth of the thoracic breadth. Beyond the fulcrum the tip of each pleura is produced to form a long, slender, free spine. The posterior margin of each pleura curves gently forwards and outwards from the fulcrum and then backwards, whilst the anterior margin curves backwards evenly and more strongly from the fulcrum to the pleural tip. The first pleural spines curve backwards only slightly, but succeeding pairs become progressively more strongly curved. The slight backward projection of each pleura at the fulcrum indicates the position of a socket which articulated with a corresponding process on the anterior margin of the succeeding pleura. The test of the thorax is almost smooth and a few minor patches of pitting are believed to be due to the state of preservation.

The pygidium is relatively large and of depressed form, its length estimated to be about one-third that of the whole exoskeleton. Its frontal margin is transversely straight, occupying about half the breadth of the posterior part of the thorax, with which it articulates by means of a pair of small bosses sited anterolaterally. The pygidium is made up of three segments, ending in markedly unequal pairs of marginal spines which occupy virtually the entire lateral margin. The axis occupies one-third of the frontal breadth of the pygidium, about two-thirds its median length (excluding the marginal spines), and tapers strongly backwards. The axial furrows are well defined frontally but become shallower posteriorly. The first two axial rings are transversely straight and well defined, but the third ring is less distinct. The first pair of marginal spines are conspicuously large and straight-sided, their long axes diverging posteriorly at about 40°. Some of the material shows longitudinal grooves

running along each spine, but these are asymmetrical and the result of crushing. The marginal spines of the second pair are slightly flattened, about one-third the size of the first pair, and only slightly divergent backwards. They are separated from the first marginal spines by broad, gently curved, shallow furrows. The third pair of marginal spines appear as continuations of the third axial ring, turning backwards through a right-angle and then running parallel to one another. They are rather less than half the length of the second pair of spines and more pointed. As far as can be judged from the rather compressed material, the first pair of pygidial spines are probably moderately inclined posteriorly, whilst both the second and third pairs are horizontal or nearly so. The second and third ring furrows of the axis are continued just beyond the axial furrows so as to form slightly elongated, pit-like depressions followed by broad, shallow grooves separating the second and third pairs of spines. The area between the third ring furrow and the posterior margin of the pygidium is slightly convex, but there is no postaxial ridge.

DISCUSSION. *Ceraurinella peregrinus* is the earliest known representative of the genus, and the only one yet described from the Arenig Series. Previously *Ceraurinella* has been found only in the Middle Ordovician (about early Caradoc Series) of North America, though Männil (1958 : 173–175, 206–207) has recorded it tentatively from slightly earlier Ordovician strata in the East Baltic region. The type species of the genus is *Ceraurinella typa* Cooper (1953 : 28–30, pl. 12, figs. 1–5, 7–8, 15–16), described originally from the Edinburg Limestone of Virginia. Cooper's type material was silicified and undistorted, so that it is impossible to make a detailed comparison of the two species in all respects. The glabellar furrows of silicified *C. typa* appear shorter (*tr.*) than those of the French species (see Cooper 1953, pl. 12, figs. 1, 3, 8 ; also Whittington & Evitt 1954, pl. 10, figs. 3, 5, 11, 12 ; pl. 13, fig. 3) but those of a crushed cephalon preserved in what was described as a "silty layer" appeared longer (*tr.*) (see Cooper 1953, pl. 12, figs. 15, 16). This variation in the length of the furrows according to preservation may be analogous to the greater length of those in *C. peregrinus*, preserved in an argillaceous matrix. Strong eye-ridges such as are developed in *Ceraurinella typa* have not been found in *C. peregrinus*. The pygidia of the two species are generally similar, but the first pair of spines are slightly less divergent in *C. peregrinus*, and the second and third axial rings are less arched in plan, ending posteriorly in spines conspicuously longer than the corresponding structures in *C. typa*.

Harper (*in* Harper & Rast 1964 : 16, pl. 2, fig. 3) has figured from the Llanvirn Series of eastern Ireland an incomplete cheirurid cranidium which he refers to the genus *Paraceraurus* Männil. The type species, *Ceraurus aculeatus* Eichwald 1860, from the Kuckers Stage of Estonia, has been described and illustrated by both Öpik (1937 : 95, pls. 13, 17–19) and Männil (1958 : 172, 206, pl. 1, fig. 1) whose photographs show certain differences from the Irish form, in which the fixigenae are narrower and the eyes are set closer to the glabella, with well developed eye-ridges running from them to the axial furrows. Harper's material is compressed and slightly distorted, and the cranidium might equally well be compared with that of *Ceraurinella*. Harper refers to, but does not figure, a pygidium said to have long first paired

pleural spines, followed by two pairs of smaller spines, the third pair being longer than the second pair. There is no mention in his reference of a terminal spine such as occurs in *Paraceraurus aculeatus*, and additional material would be needed to assess accurately the systematic position of the Irish species.

Reraspis plautini (Schmidt), also from the Kuckers Stage of Estonia, has been illustrated by Öpik (1937 : 105, pl. 11, figs. 1–5). The cephalon is broadly similar to that of *Ceraurinella*, whilst the pygidium ends in three pairs of spines, though only slightly unequal in size and lacking the extravagant development of the first pair of spines as found in *Ceraurinella*. One of the pygidia illustrated by Öpik shows the tips of the pygidial spines stepped forwards slightly from first to third, but on another of his specimens the reverse is apparently the case. An interesting feature of *R. plautini* is the overall resemblance of the hypostoma to that of *Ceraurinella peregrinus*. Both are subtriangular in plan, the lateral and posterior margins joining to form a smooth, almost parabolic curve, inside of which the median body is unfurrowed and suboval in outline. The single, damaged specimen of the hypostoma of the French species makes detailed comparison difficult, but the median body appears to be relatively a little larger, and perhaps less convex frontally. As noted earlier, the posterolateral indentations of the median body in this specimen are probably secondary.

The trilobite described from the Niti region of the Northern Himalaya by Salter (*in* Salter & Blanford 1865 : 6, pl. 1, figs. 14–18) as *Cheirurus mitis*, and later redescribed in greater detail by Reed (1912 : 106, pl. 15, figs. 10–24), has more recently been assigned to *Ceraurinella* by Kobayashi (1960 : 46). The cranidium of the Himalayan species differs from *C. peregrinus* in having the eyes sited a little farther back, opposite the second glabellar lobes, whilst the glabellar furrows are more transversely straight, a feature in which they more resemble those of *Ceraurinella typa*. In addition, the hindmost median portion of the glabella of *Ceraurinella mitis* is slightly raised and forms a conspicuous ridge-like feature, standing a little higher than the occipital ring. This ridge appears to be a primary feature of the species and not due to distortion. The pygidium of *C. mitis* resembles that of *C. typa* in having three unequal pairs of pleural spines similarly disposed, but the large spines of the first pair are more curved in *C. mitis* than in either *C. typa* or *C. peregrinus*, whilst the second pair are proportionately smaller and less flattened than in the French species, and appear to be shorter than the third pair. Kobayashi (1960 : 46) has also described *Ceraurinella* cf. *mitis* from the Ordovician of Viet Nam, and the group appears to have been very widely distributed during Ordovician times. The Asian occurrences, like those in North America, are almost certainly considerably younger than the specimens from the Montagne Noire.

Family **DALMANITIDAE** Vogdes 1890

Subfamily **ZELISZKELLINAE** Delo 1935

Genus ***ORMATHOPS*** Delo 1935

Ormathops borni sp. nov.

(Pl. 8, figs. 1–8 ; Pl. 9, figs. 1–13)

DIAGNOSIS. *Ormathops* with sub-semicircular cephalon ending posterolaterally

at genal angles carrying small fixigenal spines in immature specimens but subangular in adult stages. Glabella pentagonal in plan with transversely lozenge-shaped frontal lobe produced laterally beyond first glabellar lobes. Three pairs well-defined glabellar furrows, third pair deepest with apodemes. Glabella separated by narrow furrow from anterior border which carries frontal extension of facial suture. Palpebral lobes laterally convex, extending from axial furrows opposite first glabellar furrows until opposite middle of second glabellar lobes. Test of cheeks pitted, remainder of cephalon finely granulated. Pygidium subtriangular with short, slightly convergent axis followed by long postaxial ridge. Six axial rings present, the last two poorly defined. Side-lobes with three pairs ribs and trace of fourth pair.

Holotype. Brit. Mus. (Nat. Hist.). In.57447 (Pl. 9, figs. 4, 9, 10).

Paratypes. In.56557 (Pl. 8, fig. 8); In.56609 (Pl. 9, fig. 3); In.56613 (Pl. 9, fig. 2); In.56614 (Pl. 8, fig. 7); In.56620 (Pl. 8, figs. 1, 6); In.57446 (Pl. 9, fig. 13); In.57447 (Pl. 9, figs. 4, 9, 10); In.57448 (Pl. 8, figs. 2–4); In.57772 (Pl. 9, fig. 1); In.57898 (Pl. 9, figs. 5, 12); In.57953 (Pl. 9, fig. 11).

Other figured material. In.56588 (Pl. 9, fig. 7); It.285 (Pl. 8, fig. 5); It.286 (Pl. 9, figs. 6, 8).

Localities and horizons. All the type material was collected from locality λ16, the section by the south-eastern side of the road (Route D.136), near the southern end of the Landeyran Valley. Here and in the immediate vicinity *Ormathops borni* occurs in the Couches du Landeyran supérieures but does not range upwards into the highest strata of that subdivision. The species occurs rarely in the Couches du Landeyran inférieures and only a single cranidium and pygidium were found at locality λ33 in the hillside section 240 metres south-west of Le Foulon.

Description. The cephalon is sub-semicircular in plan, with median length slightly greater than half the maximum breadth, and only moderately convex both longitudinally and transversely. The glabella is subpentagonal in outline, broadly rounded frontally, with its maximum breadth, as measured across the frontal glabellar lobe, equal to the median length and twice the basal breadth. The frontal glabellar lobe is transversely almost lozenge-shaped and occupies about half of the glabellar length. There are three pairs of glabellar lobes, decreasing in size from first to third. The first glabellar lobes are subtriangular in outline, expanding abaxially until equal to about one-quarter of the length of the glabella. They are separated from the frontal glabellar lobe by shallow first glabellar furrows which diverge forwards at about 130° and deepen slightly near their outer ends. The second glabellar lobes are about two-thirds the size of the first lobes, subrectangular in plan and separated from the first lobes by deep, transversely straight, second glabellar furrows extending inwards almost one-third of the breadth of the glabella. The third glabellar lobes are shorter (*tr.*) than those of the second pair, subcircular in plan, expanding slightly outwards, and about one-seventh of the length of the glabella. The third glabellar furrows run inwards and slightly backwards from the axial furrows, expanding at

their inner ends, where a pair of apodemes is situated. The axial furrows are almost straight, diverging forwards at 20–25° for the most part, but are " stepped " slightly outwards so as to accommodate the frontal glabellar lobe, which projects laterally a short distance beyond the second glabellar lobes. There is also a small break in the axial furrows opposite the middle of the second glabellar lobes, the furrows being slightly more divergent forwards in front of this point. The anterior border is narrow (*sag.*), declined frontally, with gently rounded dorsal surface, and separated from the glabella by a broad (*sag.*), shallow furrow which circumscribes the frontal glabellar lobe. The border becomes slightly broader (*exsag.*) at the line of the axial furrows before narrowing again beyond them and coalescing with the lateral border to form a thickened rim extending backwards to the genal angles. The occipital ring is transversely straight and parallelsided over most of its length (*tr.*) but the ends become narrower (*exsag.*) and are developed as a pair of occipital lobes, directed anterolaterally. The occipital furrow is straight, deepening distally to a pair of apodemes. The pleuroccipital segment is narrow (*exsag.*) at the axial furrows but widens abaxially, especially beyond the fulcra, towards the genal angles where it merges with the lateral border. The genal angles are typically subangular in the largest cephala, but those of immature individuals (see p. 296) carry fixigenal spines which become progressively smaller as the size of the cephalon increases. Excluding those portions adjacent to the palpebral lobes, where they are slightly declined adaxially, the inner halves of the cheeks are almost level. The outer halves decline towards the broad, shallow, lateral border furrow, moderately near the pleuroccipital furrow but more steeply below the eyes. The palpebral lobes are abaxially convex in plan, forming thickened ridges which commence at the axial furrows opposite the outer ends of the first glabellar furrows. They then curve gently outwards and backwards, and finally inwards again so that the posterior ends are longitudinally behind the anterior ends and opposite the mid-points of the second glabellar lobes. The palpebral furrows are only slightly less convex outwards than the rims of the palpebral lobes, narrow, well defined, beginning at the axial furrows and ending by flexing around the hindmost parts of the palpebral lobes and dying out below the visual surface. The visual surfaces of the eyes are schizochroal, decline steeply abaxially, and are slightly convex overall, so that the lower boundary projects beyond the surface of the librigena, with no development of an eye-platform. In one of the largest specimens, the left eye contains approximately ninety-eight lenses arranged in seventeen vertical rows, the number per row varying from three to seven. Most of the lenses are arranged hexagonally, but some are randomly distributed. The facial suture is of proparian type. The anterior branches run forwards from the eyes, almost parallel to the axial furrows, and cut the lateral border immediately outside the anterior ends of the axial furrows. They then turn sharply inwards to meet frontally, running parallel to the frontal glabellar lobe and about one-third of the distance from it to the cephalic margin. The posterior branches curve outwards and slightly forwards for about half their length (*tr.*), and then backwards a little to cut the lateral margins at points in front of the line of the pleuroccipital furrow. Excluding the smooth furrows, most of the cephalic test is covered with closely-set,

small granules, but the surface of at least the outer halves of the cheeks is finely pitted (see Pl. 8, fig. 7). The underside of the cephalon is only partly known, but the anterior third has a doublure with a slightly convex, finely granulated, ventral surface and a median length (*sag.*) equal to one-fifth that of the glabella. The lateral parts of the doublure have not been seen and it is not clear whether a vincular furrow is developed.

The hypostoma, excluding anterior wings, is ovoid in plan, three-quarters as broad as long. The anterior margin is broadly rounded in outline with no development of a border, and is continued laterally along the front of the anterior wings, which are triangular in form and deflected dorsally. The maximum breadth of the median body is measured across the bases of the anterior wings, the outline narrowing hence to the semi-elliptical posterior margin. A narrow (*tr.*), brim-like, lateral border is developed from immediately behind the anterior wings, delimited by a narrow border furrow and coalescing with the slightly broader (*sag.*) posterior border. The ventral surface of the median body is only gently convex longitudinally but slightly more so transversely. It is divided into anterior and posterior lobes by a median furrow which is broad (*sag.*) and shallow medially, becoming notably deeper and narrower near the lateral border furrow. The median furrow is strongly arched backwards so that the posterior lobe is crescentic in shape, the ends directed anterolaterally and the maximum breadth (*sag.*) equal to one-fifth of the maximum length of the entire hypostoma.

The entire thorax has not been clearly seen, but the evidence suggests there are at least ten segments and possibly eleven, as in other species of the genus. The axis occupies one-third of the thoracic breadth and stands well above the side-lobes, which decline steeply outwards beyond the fulcra. Each axial ring is transversely straight for about three-quarters of its length (*tr.*) but forms a pair of axial lobes, divergent forwards, at the outer ends. The rings are separated from the articulating half-rings by well-developed articulating furrows. The pleurae are transversely straight for about half their projected length (*tr.*) as far as the fulcra but then become gently curved, at first backwards for a short distance and then forwards to the pleural tips. The latter are well rounded anterolaterally but angular posterolaterally, where there is a small, spinose projection, serving as a stop during enrollment of the thorax (see Pl. 8, figs. 1, 6). Each pleura is divided into two bands by a well-defined pleural furrow, beginning just in front of centre near the axial furrow and running slightly backwards and outwards so that it occupies a medial position at the fulcrum. From there it follows a sigmoidal course, flexing first gently backwards and then forwards, becoming shallower and terminating without reaching the pleural tip. The anterior band of each pleura is turned down anterolaterally to form a large facet.

The pygidium is noticeably smaller than the cephalon, its median projected length being just over half the maximum breadth, the line of which is measured across approximately the mid-point of the pygidium. The outline is subparabolic, ending in a bluntly pointed tip, whilst the frontal margin is broadly rounded in plan. The dorsal surface is strongly convex transversely and steeply declined from front to rear. The axis is straight-sided, its frontal breadth one-third of the maximum breadth of

the pygidium, and stands well above the side-lobes. The axial furrows are narrow, sharply incised, particularly frontally, and converge backwards only very slightly for two-thirds the median length of the pygidium. They then die out and the tip of the axis is difficult to define, but it merges into a postaxial ridge which declines posteriorly and extends to the tip of the pygidium (see Pl. 9, fig. 5). There are, in addition to the articulating half-ring, six axial rings separated by transversely straight ring furrows. The first two rings are well defined, but the others become progressively less so, until the fifth and sixth rings are scarcely discernible. The side-lobes are plump, moderately arched laterally, and each has an anterior half-rib, deflected anterolaterally to form a facet, followed by three pleural ribs and a trace of a fourth. Although their inner halves are deeper, the pleural furrows can be traced to the lateral margins. The interpleural furrows also reach the margins but are shallower and narrower (*exsag.*) than the pleural furrows and slightly more convex forwards in plan, dividing each rib into two nearly equal parts, of which the anterior is slightly the larger.

A few immature specimens of *Ormathops borni* were collected. Although fragmentary for the most part, they exhibit certain differences from the presumed adults of the species. Most obviously, the smallest individuals have a conspicuous pair of fixigenal spines, directed posterolaterally and, in the case of the smallest specimen, equal to more than one-third of the median length of the glabella. In addition, the palpebral lobes appear less convex outwards in plan, though of a similar length. The available evidence suggests that the smaller cephala also possessed considerably fewer eye-lenses. One specimen (see Pl. 8, fig. 8) has a pygidial length just over one-third that of the cephalon. Judging from the largest cephala and pygidia found in association it is likely that the relative size of the pygidium increased during ontogeny.

Discussion. *Ormathops* was founded by Delo (1935 : 408) on *Dalmanites atavus* Barrande (1872 : 28) from the Šárka Beds (Llanvirn Series) of Bohemia. A number of varieties, namely *intermedius*, *microphthalmus*, *transiens* and *macrophthalmus*, all of them also from the Šárka Beds, were erected by Novák (*in* Perner 1918 : 39–41) but show only small differences from *Ormathops atavus atavus*. *Ormathops borni* differs from all these in having larger, longer eyes, the visual surfaces of which are directed almost laterally instead of anterolaterally, so that the posterior ends of the palpebral lobes are situated nearer to the sides of the glabella. The first glabellar lobes of *O. borni* are relatively smaller than those of *O. atavus atavus*, and the distance between the outer ends of the first and second glabellar furrows is three-quarters of that between the second furrows and the occipital furrow. In the Czech species these two measurements are about equal. The hypostoma of *O. atavus* (Barrande 1872, pl. 15, fig. 12 ; Struve 1958, fig. 6b), though broadly similar to that of *O. borni* differs from it in having conspicuous lateral indentations behind the anterior wings, whilst the median furrow appears to be developed only laterally. The pygidia of the two species are easily separated, that of *O. atavus* being more triangular in plan, with a longer axis containing eight or so axial rings, and side-lobes made up of five and a half

pleural ribs. The corresponding numbers of rings and ribs for *O. borni* are five or five and four and a half respectively.

Whittard (1960 : 128) has redescribed *Ormathops nicholsoni* (Salter) from the Llanvirn Series of the Shelve Inlier and the Lake District. As all his illustrations show distorted specimens comparison with them is difficult, but the facial suture of *O. nicholsoni* is gonatoparian, almost marginal anterolaterally, and it is still not clear whether eyes are present or not. *Ormathops alatus* Whittard (1960 : 131), also from the Llanvirn Series of the Shelve Inlier, has a distinctively short, broad, frontal glabellar lobe, and larger first glabellar lobes than *O. borni*. In addition the fixigenae are much larger than in any other species except *O. nicholsoni*, and the eyes are situated far forwards, opposite the front of the first glabellar lobes, so that the librigenae are very small. Delo (1940 : 12) claimed that *Phacops* (now *Ormathops*) *nicholsoni* is the oldest known species of the Pterygometopinae, but the genus is nowadays assigned to the Dalmanitidae and it is clear that the Family became established earlier than was once thought. There is no record of *Ormathops* prior to the lower Arenig Series, but the genus continued thereafter with little fundamental change and has been found as high as the Llandeilo Series.

REMARKS ON THE CLASSIFICATION OF CALYMENID TRILOBITES

The systematic position of the genus *Neseuretus* [=*Synhomalonotus*] has been debated for a number of years and although the genus has generally been regarded as a calymenid, nevertheless it exhibits a number of homalonotid characters and not long ago the unhappy position was reached whereby the genus (under the name *Synhomalonotus*) was placed simultaneously in two different families in the Treatise on Invertebrate Paleontology (see Moore 1959 : O 453, 456). More recently Kobayashi (1960 : 42) has erected a Family Synhomalonotidae to accommodate trilobites of this type. The confusion concerning *Neseuretus* is, perhaps, symptomatic of the uncertainty surrounding the classification and evolution of the Calymenacea. Trilobites of this superfamily are customarily divided into two Families, Calymenidae and Homalonotidae, each of which is regarded as distinct from the other and divisible into a number of subfamilies.

The Homalonotidae are founded on the Upper Silurian (Ludlow) species *Homalonotus knighti* König, a form which is probably one of the least typical of the trilobites generally attributed to the family, possessing as it does a most unusual, and perhaps specialized, anterior border and rostral plate (see Salter 1863 : 120, pl. 12, fig. 2 ; also Reed 1918 : 275). Thus, although both *Platycoryphe* and *Brongniartella* have both been placed in the Homalonotidae (for example by Whittard 1961 : 163, and by Dean 1961 : 339, 345), it would probably be better to restrict this family to forms resembling the type genus, and to assign these two genera to a more suitable subdivision such as the Eohomalonotinae Hupé 1953, elevated here to Family rank. Although a revision of the Silurian and Devonian genera is still awaited it is likely that many of them at least, for example, *Trimerus*, *Dipleura*, *Burmeisterella*, *Digonus* and *Burmeisteria*, could be accommodated satisfactorily within the Trimerinae Hupé 1953, another subfamily which may well merit Family rank.

Certain Tremadoc genera, for example *Pharostomina* and *Euloma*, have from time to time been put forward as strong contenders for the role of calymenid ancestor or ancestors, but the fact remains that early in the Arenig series the Calymenacea were already established as a number of distinct groups, and whether they be called families or subfamilies is somewhat arbitrary. Subsequently these groups pursued lines of descent through part, or in some cases most, of the Ordovician succession and often showed but little structural modification in the process. In this part of the geological column it is difficult to differentiate reliably between so-called calymenid and homalonotid trilobites, and some groups exhibit a combination of features which have often been regarded as diagnostic of one family or the other. For example, the calymenids *sensu stricto* are characteristically gonatoparian (though exceptionally proparian in at least one species of the genus *Flexicalymene*) with three pairs of well-developed, unequal glabellar lobes, and mostly without a discrete preglabellar field. On the other hand the homalonotids, at least in the Ordovician, typically possess a trapezoidal or subtrapezoidal glabella, sometimes with glabellar furrows, and a scoop-like anterior border. In addition, a pair of paraglabellar areas has been said by Whittington (1965) to be typical of homalonotids. Such structures are certainly lacking in calymenids *sensu stricto*, but they are also strongly developed in *Bathycheilus* whilst the usually described " posteriorly expanded axial furrows " of *Prionocheilus* [=*Pharostoma*] must surely now be interpreted as paraglabellar areas. These last two genera have glabellar outlines and furrows approaching those of the calymenids, accompanied, however, by a distinct preglabellar field and a well-developed opisthoparian facial suture. They stand apart from both calymenids and homalonotids. In classifying the members of the Calymenacea there are a number of courses open. One could continue to use the twofold subdivision already mentioned, but this ignores the number of genera which possess characters of both calymenid and homalonotid type. Alternatively, to " lump " all the genera together as calymenids would certainly be over-simplifying the problem. For the purposes of the present paper it is preferred to utilize a number of families, all of equal rank within the Superfamily Calymenacea. This procedure recognizes that during the early part of the Ordovician a number of cryptogenetic genera appeared and thereafter evolved for varying lengths of time and often in different geographical provinces. It is possible that the Calymenacea may eventually prove to be polyphyletic.

Family **BATHYCHEILIDAE** Přibyl 1953

1953. Pharostomidae Hupé : 232.

Genus ***BATHYCHEILUS*** Holub 1908

Bathycheilus gallicus Dean

(Pl. 10, figs. 4, 8–12)

1965. *Bathycheilus gallicus* Dean : 5, pl. 2, figs. 1–9.

Localities and horizon. *Bathycheilus gallicus* has been found at only two localities, $\lambda 2$ and $\lambda 4$, in the Landeyran Valley and is uncommon there. The species

is more abundant at the hillside section 250 metres south-west of Le Foulon, where it was found at $\lambda 30$, $\lambda 32$ and $\lambda 33$, especially the last. All these localities are in the Couches du Landeyran inférieures, and *B. gallicus* is also known from presumably the same horizon in the Boutoury district, farther north-east.

FIGURED MATERIAL. Guiraud Coll., University of Montpellier (Pl. 10, fig. 4); Brit. Mus. (Nat. Hist.) In.57482 (Pl. 10, fig. 8); In.57483 (Pl 10, fig. 12); It.165 (Pl. 10, fig. 9); It.166 (Pl. 10, fig. 10); It.167 (Pl. 10, fig. 11).

DESCRIPTION. This characteristic and easily recognized species from the Couches du Landeyran inférieures has already been described and discussed in detail, so that little need be added. Since the original description, a hypostoma of appropriate type has been found in association with fragments of undoubted *B. gallicus* and is assigned tentatively to the species. The hypostoma of *Bathycheilus* has not previously been described, so some doubt as to the identification must remain. The median body is slightly more than one and a half times as long as broad, and is divided into two lobes by a median furrow. The latter is deep and broad (*exsag.*) at its outer ends where it indents the lateral margins of the median body, running backwards and inwards to follow a semi-elliptical path across the median body, and becoming almost obsolete medially. The anterior lobe so formed is ovoid in plan, slightly more convex frontally than posteriorly, and about as broad as long. The posterior lobe of the median body has a maximum breadth little more than twice the maximum length (measured near the outer ends) and is almost reniform in plan, with the posterior margin slightly indented medially. The anterior border, though incompletely preserved, is narrow (*sag.*), brim-like, probably arched forwards moderately, and separated from the median lobe by a broad (*sag.*), shallow furrow. It is confluent laterally with the anterior parts of the anterior wings, the latter forming large, subrectangular processes which have a flattened surface and are obliquely truncated at their outer ends. The hindmost parts of the anterior wings are continued backwards to form the lateral borders, ridge-like in form and sigmoidal in plan so as to form a pair of lateral notches in the hypostomal outline. They curve inwards again posteriorly to join the posterior border, which is slightly lower and broader (*sag.*), though obsolete medially where the posterior margin is cut by a large, curved notch, so that the hypostoma is notably bifurcated. The lateral border furrows are continuous with the anterior border furrow, but markedly narrower (*tr.*) and deeper over their frontal halves. They become shallower opposite the ends of the posterior lobe of the median body but deepen again beyond them, finally shallowing a little as they sweep inwards to join the posterior border furrow.

DISCUSSION. Gigout (1951 : 290, pl. 3, figs. 8–10) noted certain Ordovician trilobites from Morocco as "*Calymene* (*Pharostoma?*) aff. *pulchra* Barrande" and stated that they had earlier been recorded by H. & G. Termier (1950, pl. 189, figs. 19, 21) as both "*Synhomalonotus* sp." and "*Metacalymene? declinata* Barrande". Gigout claimed that his fragments from Morocco were identical with undescribed specimens, including whole individuals with long genal spines, from Boutoury, Hérault, in Thoral's collection. According to Gigout, although Thoral had compared

these specimens to *C. pulchra* they were not, in fact, identical with that species, being much smaller and without a spinose border. I have seen in the University of Montpellier some of the specimens from Boutoury available to Thoral and labelled as "*Pharostoma*", and it is clear that they are typical examples of *Bathycheilus gallicus*. As I have not had the opportunity of examining Gigout's rather damaged Moroccan material it is not definitely known whether he was dealing with the same species as that from the Montagne Noire, but there is a strong resemblance, as far as can be judged.

Genus ***PRIONOCHEILUS*** Rouault 1847

1847. *Pharostoma* Hawle & Corda : 88.

Certain authors have assumed that *Pharostoma* had priority over *Prionocheilus*, in spite of the fact that the type-material of the type-species *P. verneuili* Rouault 1847 was refigured by Bézier (1907 : 120), who also affirmed that *Prionocheilus* had the earlier date of publication and should therefore be retained. The position has recently been reviewed (Dean 1964) and the prior claim of *Prionocheilus* recognized. The genus has an extended vertical range, occurring as early as the Arenig Series, whilst the last-known representatives are found in the Ashgill Series.

Prionocheilus matutinus sp. nov.

(Pl. 10, figs. 1, 2, 3, 6, 7)

Diagnosis. Species of *Prionocheilus* with glabellar outline well-rounded, broader than long. Three pairs glabellar lobes generally present, those of first pair poorly defined and sometimes obsolete. Second and third pairs of lobes markedly unequal in size, with slight "step" in glabellar outline in front of second lobes. Eyes sited opposite first glabellar furrows and anterior part of anterior glabellar lobes. Ocular ridges poorly developed. Preglabellar field small. Lower surface of librigenae with row of small, ventrally-directed spines.

Holotype. Brit. Mus. (Nat. Hist.) In.57434 (Pl. 10, fig. 7).

Paratypes. In.57428 ; In.57430 (Pl. 10, fig. 3) ; In.57431 ; In.57486 (Pl. 10, fig. 2) ; It.162 (Pl. 10, fig. 1) ; It.164 (Pl. 10, fig. 6).

Locality and horizon. The species has so far been found at only one locality, λ2 near the northern end of the Landeyran Valley (see Text-fig. 3). The horizon is in the Couches du Landeyran inférieures.

Description. The cranidium is almost twice as broad as long, moderately convex transversely and longitudinally. The glabella is semi-elliptical in outline, the median length about four-fifths of the basal breadth. There are three pairs of unequal glabellar lobes. The basal lobes are the largest, their length about half that of the glabella, and three-quarters as broad as long. In outline the basal glabellar lobes are of the "cat's ear" plan so well known from many Calymenacea, that is to say rounded posteriorly but angular anterolaterally. The second glabellar

lobes are subcircular and slightly less than half the length of the basal lobes. The third glabellar furrows are deep and narrow, and do not quite reach the axial furrows, so that both pairs of glabellar lobes are conjoined abaxially. The third furrows then run slightly backwards adaxially until level with the inner boundary of the anterior glabellar lobes, when they bifurcate. The anterior branches so formed are short, deep at first but shallowing to cross the " necks " linking the second glabellar lobes with the median body of the glabella. The posterior branches are long, curving backwards strongly and ending only a short distance in front of the occipital furrow. The so-called " oval areas " at the inner ends of the third glabellar furrows noted for this genus by Whittington (*in* Moore, 1959 : O 454) are almost unknown in *P. matutinus*, probably owing to the state of preservation. The second glabellar furrows are short (*tr.*), straight at first, directed backwards and inwards, but then turning through a right-angle before ending abruptly opposite the mid-points of the second glabellar lobes. The first glabellar lobes are very small and often almost indiscernible. The axial furrows are gently curved, convex outwards, deep and uniformly narrow over most of their length but constricted slightly opposite the second glabellar lobes and again just behind the line of the outer ends of the third glabellar furrows. From there to the occipital furrow they become united with a pair of paraglabellar areas, longitudinally semi-elliptical in outline, flat-bottomed and set below the dorsal surface of the fixigenae but level with the lower limit of the axial furrows. The curved abaxial margins of the paraglabellar areas are almost vertical and they end posteriorly at the junction of the axial and occipital furrows. The position of the paraglabellar areas coincides with the structures described as " pharostomian scars " in the Estonian species *Prionocheilus* [*Pharostoma*] *nieszkowskii* (Schmidt) by Öpik (1937 : 23 ; see also Hupé 1953 : 72, and Harrington *in* Moore 1959 : O 95–97). The frontal glabellar lobe is broadly rounded, circumscribed by a narrow (*sag.*), well-defined preglabellar furrow which separates it from a small preglabellar field. The last-named narrows (*sag.*) adaxially and is only faintly convex ; it is delimited frontally by an anterior border furrow which is strongest laterally, where it apparently merges with the lateral border furrow, but is much less well developed medially. The anterior border is about half the height of the frontal glabellar lobe, rounded in cross-section and moderately inclined forwards. The lateral border is known only from an incomplete left librigena. It is low, rounded in cross-section, and separated from the inner portion of the cheek by a sharply-incised lateral border furrow. The ventral surface carries a rake-like structure formed by the development of a single row of small spines, directed ventrally and arranged longitudinally (see Pl. 10, fig. 2). Whittington (*in* Moore 1959 : text-fig. 357), in a reconstruction of the genus, shows similar spines extending only along the ventral side of the librigenae, but specimens of *Prionocheilus* from Bohemia, in the British Museum (Natural History), as well as others figured by Whittard (1960, pl. 18, figs. 2–4, 6) from West Shropshire show clearly the continuation of the row across the ventral surface of the rostral plate. The occipital ring is transversely straight and parallelsided for the most part, with a trace of a small median tubercle, but abaxially it narrows owing to indentation by the posterior margins of the third glabellar lobes,

and forms a pair of occipital lobes, directed anterolaterally towards the posterior ends of the paraglabellar areas. The occipital furrow is narrow (*sag.*) and deep, transversely straight over its median third but then curves around the third glabellar lobes. The pleuroccipital furrow meets the axial furrows well behind the line of the median third of the occipital furrow. It is fairly narrow (*exsag.*) and almost straight-as far as the fulcra, where it becomes progressively broader and curves backwards gently to meet the lateral border furrows. Correspondingly the pleuroccipital segment is almost uniformly narrow (*exsag.*) as far as the fulcra but then increases gradually in breadth as it curves gently backwards and outwards ; its outer ends are not known. The genal angles and, presumably, librigenal spines are not known. The palpebral lobes are small, situated opposite the second glabellar lobes. They decline gently inwards and are scarcely differentiated from the fixigenae. From the palpebral lobes the anterior branches of the facial suture run forwards, gently convergent and subparallel to the axial furrows, to cut the anterior border approximately in-line longitudinally with the outer margins of the paraglabellar areas before running slightly below the top of the anterior border to meet frontally. The rostral plate is not preserved. The posterior portions of the fixigenae are moderately declined laterally, and the posterior branches of the facial suture are strongly arched backwards, though their outer ends have not been found preserved. Although the palpebral lobes are sited at the apices of the fixigenae, there is no development of eye-ridges such as occur sometimes in other species of *Prionocheilus*. The surface of most of the test, excluding furrows, is ornamented with closely-grouped tubercles, both small and of medium size, the larger ones often showing traces of a median perforation. The lateral border is finely granulated, whilst the preglabellar field carries only a few, more widely distributed, larger tubercles.

The hypostoma is not known.

The thorax is fragmentary and poorly preserved but appears to be typical for the genus. There are thirteen thoracic segments and one specimen shows the surface of the test, excluding the furrows, to be covered with granules similar to those on the pygidium.

The pygidium is represented by a single, small specimen (see Pl. 10, fig. 3). When held with the pygidial axis horizontal the median length of the pygidium, excluding the articulating half-ring, equals two-thirds of the maximum breadth, and the frontal margin is strongly arched forwards. The posterolateral margins are slightly convex and gently rounded, their curvature in-line with the broadly-rounded tip of the pygidium. Frontally the axis occupies one-third of the total pygidial breadth. It tapers only slightly for two-thirds of its length but then more sharply to the bluntly-pointed tip, which does not reach the posterior margin. The axial furrows are broad and deep frontally, becoming narrower posteriorly and circumscribing the axial tip. There is no postaxial ridge. Excluding the articulating half-ring there are five axial rings, the fifth less well defined than the others, followed by a large, subtriangular terminal piece. The side-lobes carry, in addition to the anterior pair of half-ribs, four more or less well-defined pairs of pleural ribs, with traces of a fifth pair. The ribs are separated by deep, narrow pleural furrows which arch backwards strongly,

and the first three pairs of ribs carry interpleural furrows which are best developed immediately outside the axial furrows. The surface of all the pygidium, apart from the various furrows, is conspicuously granulated.

DISCUSSION. *Prionocheilus* has an extremely long vertical range and is known throughout most of the Ordovician, from the Arenig to the Ashgill Series. The numerous species described have been noted (as *Pharostoma*) by Whittard (1960 : 137) and the points of difference assessed.

Prionocheilus pulcher (Beyrich) is reputed to extend from the Llanvirn to the Caradoc Series in Bohemia, but in South Wales and the Shelve Inlier it is known only from the Lower Llanvirn. The species, which appears to be larger than *P. matutinus*, has a slightly broader glabella with more clearly defined first glabellar lobes, a longer (*sag.*) preglabellar field, and eyes which are sited a little farther forwards, at the outer ends of distinct ocular ridges. The pygidium of *P. matutinus* is arched forwards more strongly in plan than that of *P. pulcher*, and the side-lobes have only four pairs of pleural furrows compared with six in the Bohemian species. The axial furrows of *P. pulcher* converge backwards to the third ring furrow and then run parallel, whereas in *P. matutinus* the axis narrows gently and uniformly backwards to the bluntly-pointed terminal piece. There are five axial rings in *P. matutinus* and six in *P. pulcher*. The Bohemian subspecies from the Šárka Beds (Llanvirn Series), separated by Šnajdr (1956 : 29) as *Pharostoma pulchrum vokovicense* can be easily distinguished by its well-developed preglabellar field, the anterior half of which is flat and smooth whilst the posterior half forms a transverse ridge ornamented with granules like those on the remainder of the cephalic test.

Prionocheilus verneuili Rouault (1847, pl. 3, fig. 3) from Brittany has been refigured by Bézier (1907). Some of the differences between this species and *P. pulcher* have been noted by Whittard (1960 : 137), but Rouault's type-material at Rennes University shows clearly that the eyes of *P. verneuili* are opposite the second glabellar lobes, that is, in a position similar to those of *P. pulcher*. The anterior border of *P. verneuili* is a little longer than in the Czech species and less distinct from the preglabellar field, though the anterior border furrow may have been obscured by crushing. A feature which is not made clear by Bézier's photographs, owing to the angle at which the specimen was illuminated, is the manner in which the front of each third glabellar lobe is partly fused with the back of the adjacent second lobe, the second glabellar furrows being reduced to shallow depressions. I have seen a similar development of the second glabellar furrows in stratigraphically younger specimens of *Prionocheilus* from Czechoslovakia, but they are deeper in specimens from the Llanvirn Series of both Britain (Whittard, 1960 : 135) and Bohemia (see *P. pulcher vokovicensis* Šnajdr ssp., 1956 : 29). The third glabellar lobes of *P. verneuili* are slightly longer than those of *P. pulcher* and, as far as can be judged, the paraglabellar areas of the Breton form are larger and broader than those in other species. When illustrating Rouault's species, Bézier utilized not only the type-material from Poligné but also better-preserved specimens from the well-known locality of Le Traveusot, and it is not clear whether the horizons or species are identical. A crushed pygidium

in Rouault's collection from Poligné indicates seven axial rings and six rib furrows, apparently more than are shown in Bézier's specimens from Traveuzot. *Prionocheilus matutinus*, probably a smaller form than *P. verneuili*, has a narrower glabella, shorter anterior border, and a much less well-developed preglabellar field. The eyes occupy a similar position in the new species but lack strong ocular ridges, whilst the paraglabellar areas are smaller. The pygidium of *P. matutinus* has fewer axial rings and pleural furrows than that of *P. verneuili*.

Immature cranidia of *Prionocheilus matutinus* bear some resemblance to the genus *Colpocoryphoides* Harrington & Leanza (1957 : 222–224), founded on *Pilekia trapezoidalis* Harrington (1938 : 191, pl. 6, fig. 22) from the Upper Tremadoc and Lower Arenig of Argentina. The glabella of *C. trapezoidalis* is more truncated frontally, however, and has three well-defined pairs of glabellar lobes, but the anterior border and small preglabellar field are reminiscent of those in *P. matutinus* whilst certain of Harrington & Leanza's illustrations show a slight posterior widening of the axial furrows, suggesting the possibility of paraglabellar areas. Whittington (*in* Moore 1959 : O 453) placed *Colpocoryphoides* in the synonymy of *Pharostomina* Sdzuy (1955 : 31), from the Leimitz-Schiefer (Tremadoc Series), an assertion accepted by Harrington & Leanza in an addendum to their 1957 paper. Certain of the illustrations of the type-species *Pharostomina oepiki* Sdzuy (1955, pl. 6, figs. 62–75) exhibit what appear to be moderately developed paraglabellar areas.

Family **COLPOCORYPHIDAE** Hupé 1955

Genus ***COLPOCORYPHE*** Novák *in* Perner 1918

Vanêk (1965) placed *Colpocoryphe* in the synonymy of *Plaesiacomia* Hawle & Corda 1847. I prefer to maintain the two as separate genera, and propose to discuss the problem in detail at a later date.

Colpocoryphe thorali sp. nov.

(Pl. 10, fig. 5 ; Pl. 11, figs. 1–10 ; Pl. 12, figs. 1–11)

DIAGNOSIS. Species of *Colpocoryphe* with bell-shaped glabellar outline and three pairs unequal glabellar lobes, first pair smallest and poorly defined. Breadth of frontal glabellar lobe two to three times median length. Anterior border short (*sag.*) medially, expanding anteroventrally in front of axial furrows. Eyes almost pedunculate, close to glabella, opposite first pair and front half second pair glabellar lobes. Librigenae large, convex. Hypostoma bifid, with lateral margins indented behind anterior wings ; median body divided into two unequal lobes. Thorax of thirteen segments. Pygidium convex, subtriangular, with six or seven axial rings on internal mould ; fewer rings show on external mould. Side-lobes with one or two pairs pleural furrows and pair of deep marginal furrows forming vincular attachment with margins of librigenae.

HOLOTYPE. Brit. Mus. (Nat. Hist.) In.56654 (Pl. 12, figs. 2, 6, 9).

PARATYPES. In.57438 (Pl. 12, fig. 3) ; In.57552 (Pl. 12, fig. 1) ; In.57586 (Pl. 11, fig. 6) ; In.57622 (Pl. 11, fig. 1).

OTHER FIGURED MATERIAL. In.57498 (Pl. 11, fig. 7) ; In.57502 (Pl. 12, fig. 10) ; In.57504 (Pl. 11, fig. 9) ; In.57510 (Pl. 11, fig. 5) ; In.57516 (Pl. 12, fig. 11) ; In.57594 (Pl. 12, fig. 4) ; It.168 (Pl. 10, fig. 5) ; It.170 (Pl. 11, figs. 2, 10) ; It.171 (Pl. 11, figs. 3, 8) ; It.172 (Pl. 11, fig. 4) ; It.173 (Pl. 12, figs. 5, 8) ; It.174 (Pl. 12, fig. 7).

LOCALITIES AND HORIZONS. The holotype and two of the paratypes were collected from locality λ16, south-east of the road in the southern part of the Landeyran Valley, whilst the remaining paratypes are from the nearby λ20. Both localities are in the Couches du Landeyran supérieures, strata in which *Colpocoryphe thorali* is abundant and almost ubiquitous, so that it is not proposed to list the numerous places at which it occurs. The species occurs also in the Couches du Landeyran inférieures, but in notably smaller numbers. It was found in the northern part of the Landeyran Valley at λ2 and λ4, as well as at localities λ30 to λ33, especially λ32, in the hillside section 240 metres south-west of Le Foulon. Uncommon fragments of *Colpocoryphe* from the Couches du Foulon, though too poorly preserved for certain identification, are generally similar to the new species.

DESCRIPTION. The entire dorsal exoskeleton is longer than broad approximately in the ratio 8 : 5, the maximum breadth being measured across the cephalon at the line of the pleuroccipital furrow. The cephalon is semicircular in plan with the dorsal surface moderately declined forwards and strongly convex transversely. The glabella is plump, standing well above the fixigenae, and bell-shaped in plan with projected length and breadth approximately equal. It is bounded by axial furrows which are deep and narrow, subparallel over their anterior halves but divergent posteriorly at 45–50° from just behind the second glabellar furrows. Three pairs of unequal glabellar lobes increase in size from the first to third lobes. The third glabellar lobes are the largest, about one-third of the projected length of the glabella and generally subcircular in plan but angular anterolaterally. The lobes are joined to the median body of the glabella by broad (*exsag.*) " necks " which equal half their own length (*exsag.*) and have a convexity continuous with that of the third lobes. The posterior margins of the third lobes are slightly convex backwards, indenting the occipital furrow and ring. The third glabellar furrows are broad (*exsag.*) and uniformly deep, arching inwards and backwards from the axial furrows to end opposite the centre of the third lobes. In certain internal moulds of crushed specimens the third furrows appear straighter than has been described. The second glabellar lobes are subrectangular, their long axes broadly divergent forwards and their tips level with the centres of the third lobes. The second glabellar furrows are sited a little in front of centre of the glabella and are deepest at the axial furrows, becoming shallower as they curve adaxially and slightly backwards to end in-line with the third furrows. The second furrows show clearly on internal moulds, but on external moulds they often appear as little more than notches in the glabellar outline. The first glabellar lobes are almost as long (*exsag.*) as the second lobes but appear smaller

on account of the poorly-defined first glabellar furrows which form narrow (*exsag.*), almost straight incisions extending only a little way from the axial furrows. The frontal glabellar lobe is subrectangular in plan, rounded anterolaterally, and generally with an almost straight anterior margin, though some specimens have a shallow (*sag.*) concavity which gives the suggestion of a pair of anterolateral lobes. A similar feature has been noted on certain specimens of *Neseuretus* (see p. 311). There seems to be a small amount of variation in the length of the frontal glabellar lobe, ranging from almost half to one-third of its maximum breadth, and the lateral margins of the shorter examples are slightly more convergent forwards than those of the longest. However, it has not been established that such extremes represent more than normal variation within the species, as they occur in specimens which are otherwise identical, and have been found both separately and in association throughout a large thickness of strata. Immediately in front of the frontal glabellar lobe, and separated from it by only a shallow groove, is a smooth, slightly convex border which declines forwards almost vertically to the cephalic margin. In anterior view the frontal margin of the cranidium is strongly arched transversely, giving the impression of being bifid with a large median indentation, owing to the development of a pair of rounded projections directed forwards and almost vertically downwards in front of, and adjacent to, the axial furrows (see Pl. 11, fig. 2 ; Pl. 12, fig. 5). The function of these structures is discussed later. The median two-thirds of the occipital ring are parallel-sided, their length (*sag.*) one-fifth that of the glabella ; abaxially the ring becomes shorter and curves forwards slightly to form a pair of occipital lobes which end level with the third glabella lobes. The occipital furrow is fairly shallow medially but deepens laterally to a pair of apodemes. The pleuroccipital segment is narrow (*exsag.*) immediately outside the axial furrows, but expands uniformly to twice this breadth just beyond the fulcra before narrowing more sharply at the rounded genal angles. The pleuroccipital furrow is transversely straight, broad (*exsag.*) and moderately deep for the most part, but becomes shallower abaxially where it turns forwards and is continuous with the lateral border furrow. The latter is developed posteriorly as a broad, shallow groove which quickly becomes obsolete. The eyes are almost pedunculate, situated well forwards opposite the first pair and the anterior half of the second pair of glabellar lobes, and only a short distance from the axial furrows. The palpebral lobes are abaxially convex without palpebral furrows ; they stand almost as high as the glabella and decline steeply towards the axial furrows. Some specimens show traces of a pair of ocular ridges, but these parts of the test are generally obscured by crushing. The visual surfaces of the eyes are holochroal and in lateral view are seen to decline forwards slightly. No estimate of the number of eye lenses present has yet proved possible. The eyes are separated from the librigenae by broad, rounded furrows but no definite eye-platform is developed. The anterior branches of the facial suture run forwards from the eyes, diverging very slightly from the axial furrows until beyond the front of the glabella, where they flex inwards to circumscribe the bifid anterior projections of the cranidium which were described earlier, and finally curve backwards to meet at the apex of the median indentation of the anterior border. The posterior branches of the facial suture arch

uniformly outwards and back from the eyes to cut the genal angles, delimiting large fixigenae which have their outer two-thirds turned-down abaxially. The librigenae are steeply declined and in certain less distorted specimens their plump dorsal surfaces project as far as, or even beyond, the lateral margins. They are approximately triangular in outline with curved boundaries, the lateral margin convex, the other sides slightly concave. The anterolateral angles are produced to form a pair of hook-like extensions which curve inwards and back ; they were originally linked by a narrow strip of the test, but this part of the exoskeleton is almost invariably obscured by crushing. The surface of the glabella, occipital ring, cheeks and pleuroccipital segment is covered with small, closely-set granules but it is not clear whether such ornamentation extended over the anterior border.

The hypostoma, excluding anterior wings, is about two-thirds as broad as long, its ventral surface only moderately convex. The frontal margin is broadly arched forwards, continuous with that of the anterior wings which are long (*tr.*), subtriangular in plan, and deflected dorsally, particularly over their outer halves. Immediately behind the anterior wings the hypostomal outline narrows slightly but then expands to attain its maximum breadth a little behind centre. Beyond this point the outline narrows more sharply to the bifid posterior margin. There, the posterior wings are triangular, separated by a narrow median notch whose length (*sag.*) is almost one-sixth that of the entire hypostoma. The median body is divided into two lobes by a median furrow which is semi-elliptical, concave forwards and shallow medially, becoming deeper and narrower (*exsag.*) abaxially. The anterior lobe is ovoid in outline, its frontal margin bounded by a broad (*sag.*), poorly defined anterior border which narrows medially and fuses abaxially with the anterior wings. The swollen posterior lobe is crescentic in plan and its maximum breadth (*tr.*) exceeds that of the anterior lobe in the ratio 5 : 4. The median body is bounded laterally by a deep, narrow border furrow which shallows a little posteriorly. The lateral border is narrow and ridge-like immediately behind the anterior wings, with which it coalesces, but becomes broader posterolaterally and is continuous with the posterior wings.

The thorax consists of thirteen segments. The axis is broad, occupying almost half the projected thoracic breadth, and is bounded by deep, broad axial furrows. The axial rings are about six times as broad as long (*exsag.*), flexing slightly backwards and then forwards abaxially to end in a pair of weak axial lobes. Each has a well-developed articulating half-ring and furrow. The pleurae are horizontal for about half their length (*tr.*) but turn down through almost a right-angle. They are transversely straight as far as the fulcra, but then curve slightly backwards and forwards again, their anterolateral margins being deflected ventrally to form articulating facets. Each pleura carries a narrow (*exsag.*) pleural furrow which appears broader on the internal mould and runs from the anterior margin at the axial furrow. The pleural furrow is directed slightly backwards abaxially until beyond the fulcrum, where it curves forwards slightly and dies out without attaining the pleural tip, which is rounded for the most part but subangular anterolaterally.

The pygidium is transversely convex, steeply declined posteriorly when uncrushed, and quadrant-shaped in plan with well-rounded anterior margin. The lateral mar-

gins meet at a blunt point and are generally straight, though some material shows them slightly concave posteriorly. The axis stands conspicuously higher than the side-lobes and is bounded by axial furrows which appear deep and broad on the internal mould but are less conspicuous on the external mould. Similarly, the axial rings are better defined in the case of internal moulds, and the number of rings present is six, with traces of a seventh, in one of the largest specimens so preserved, though only two are clearly visible on the corresponding external mould. The axis narrows more strongly posteriorly but continues almost to the tip of the pygidium and forms a conspicuous terminal piece. The side-lobes are arched downwards abaxially and each generally shows only traces of one or two pleural furrows. Their most conspicuous feature, however, is a pair of deep, broad furrows which run parallel to the lateral margins and continue posteriorly, becoming slightly concave in plan abaxially, so as to indent the lower part of the hindmost third of the axis, giving it an undercut appearance. These furrows are a characteristic feature of *Colpocoryphe* and it is now clear that they are vincular structures. During enrollment of the exoskeleton the terminal piece of the pygidial axis engaged with the median indentation of the front of the cephalon. At the same time the margins of the librigenae overlapped the ridge-like pygidial margins and came to rest in the marginal furrows and against the undercut posterior part of the axis. The result must have been an extremely efficient form of fastening. It is interesting that a superficially similar pair of anterior cephalic projections was illustrated by Brøgger (1882, pl. 5, figs. 1, 2) for *Cheirurus clavifrons* Dalman, a species now assigned to *Cyrtometopus*. These structures may also have functioned during enrollment but differ fundamentally from those of *Colpocoryphe* by being developed from the rostral plate. The surface of at least the lateral portions of the pygidium of *C. thorali* is ornamented with small granules like those of the cephalon.

Several immature specimens of *Colpocoryphe thorali* were collected, most of them in a fragmentary condition and all either meraspides or small holaspides. They were found at a variety of localities and horizons, but λ19, in the Couches du Landeyran supérieures near the southern end of the Landeyran Valley, proved particularly fruitful. The smallest specimen, not figured here, is a very small Meraspis from the Couches du Landeyran inférieures at locality λ2. It is a cranidium, In. 57433, preserved as an internal mould, with a basal breadth of 0·8 mm. and a median length of approximately 0·5 mm. The glabella is subcylindrical and conspicuously narrow, about 0·125 mm. The eyes are sited close to the glabella almost at its anterior end, and the occipital ring is small and short with traces of a pair of apodemes in the outer ends of the occipital furrow. Slightly larger cranidia about 1 mm. broad (see Pl. 11, figs. 5, 7) show a generally similar form but the glabella is more depressed and relatively broader, almost one-quarter of the total breadth. Even in the later stages of the Meraspis the glabellar outline is still subrectangular (for example Pl. 11, fig. 9), but the palpebral lobes occupy a position corresponding to that in the adult, although they appear to be slightly larger. In specimens of Meraspis Degree 11 (Pl. 11, fig. 9) the glabellar lobes are visible, though indistinct, but become progressively better defined later, the posterior part of the glabella expanding laterally at the same time.

Discussion. The type species of *Colpocoryphe* was described as *Calymene arago* (a name frequently misquoted as *aragoi*) by Rouault (1849 : 88, pl. 2, fig. 3). Unfortunately his material, which came from cleaved dark mudstones at La Couyère, Brittany, comprised specimens which had been more or less distorted, and the species still awaits redescription in modern terms. *Colpocoryphe arago* was figured from a number of horizons and localities other than the type by several authors including de Verneuil & Barrande (1855 : 973), using Spanish material, and later by Barrande (1872 : 34) from Bohemia though his specimens are now referable to *Colpocoryphe bohemica* Vaněk sp. (1965 : 26). Descriptions such as these seem to have formed the basis of all subsequent interpretations of *C. arago*, and this must be borne in mind when comparing the species with others. Judging from Breton specimens preserved uncrushed in siliceous nodules, *Colpocoryphe arago* is a notably larger species than *C. thorali*, generally with a slightly shorter, broader glabella and eyes which are smaller, shorter and set slightly lower in relation to the glabella. The pygidia of the two species are broadly similar but that of *C. arago* has a narrower, more convex axis and the inner parts of the side-lobes are slightly larger. The terminal piece of the Breton species appears to be thicker and more conspicuous, but this part of the exoskeleton is difficult to compare owing to crushing in the material from the Montagne Noire.

Colpocoryphe salteri (Rouault 1851 : 358) from the Ordovician of Brittany has a broader, more convergent glabellar outline than either *C. arago* or *C. thorali*, and the eyes appear to be placed even farther forwards, opposite the first glabellar lobes. The pygidium of this species is distinctive, conspicuously large, with a narrow axis and plump side-lobes which carry traces of numerous pleural furrows and have the vincular furrows only lightly impressed midway between the axial furrows and the lateral margins. Thadeu (1949) has recorded this species, as *Synhomalonotus salteri*, from the Bussaco and Valongo districts of Portugal, but after an examination of Rouault's type material at Rennes University I agree with Pillet (*in* Cavet & Pillet 1964 : 324) that it belongs with *Colpocoryphe*, as does *Synhomalonotus lusitanica* Delgado MS., also from Valongo (Thadeu 1949 : 7).

The holotype of *Calymene* (*Colpocoryphe*) *grandis* Šnajdr (1956 : 25) is a cranidium about twice the size of the largest available specimens of *C. thorali*, from which it differs in having a more trapezoidal glabellar outline, deeper glabellar furrows and eyes set slightly farther back. One of the paratypes of *Colpocoryphe grandis* is a large cephalon in which the glabellar outline broadens slightly behind the second glabellar lobes, as in *C. thorali*, but the frontal glabellar lobe expands anterolaterally to form a fairly distinct pair of lobe-like projections. There are also traces of a fourth pair of glabellar lobes. *C. grandis* occurs in the Drabov and Letná Beds of Bohemia and is therefore stratigraphically much later than *C. thorali*. Another Bohemian species *Colpocoryphe inopinata* (Novák *in* Perner, 1918 : 10, 36) from the Šárka Beds (Llanvirn Series) is easily distinguished by its strongly convergent, almost subtriangular, glabellar outline and the unusually anterior position of the eyes, opposite the frontal half of the frontal glabellar lobe.

Gigout's record (1951 : 280) of *Colpocoryphe arago*, associated with *Plesiomegalaspis*

graffi Thoral (described from the Arenig Series of the Montagne Noire) suggests that *C. thorali* might occur in certain North African faunas.

Family **SYNHOMALONOTIDAE** Kobayashi 1960

Genus ***NESEURETUS*** Hicks 1872

1898. *Synhomalonotus* Pompeckj : 240.

Neseuretus ramseyensis Hicks 1872 was designated as type species of the genus by Vogdes (1925 : 106), but Whittard (1960 : 139) has shown this specific name to be a junior subjective synonym of *Neseuretus murchisoni* (Salter 1865). Hicks's genus remained either overlooked or misunderstood for many years until redescribed by Whittard (1960 : 138), who demonstrated that *Neseuretus* is a subjective synonym of, and has priority over, *Synhomalonotus* Pompeckj 1898. Nevertheless the familial name Neseuretidae cannot be used while Article 40 of the International Code of Zoological Nomenclature remains in force. The type-specimens of *Calymene tristani* Brongniart (1822 : 12), the type-species of *Synhomalonotus*, were refigured by Pompeckj (1903). They came from the so-called " Schistes à Calymènes " in their characteristic development in the Contentin Peninsula, at the western end of Normandy, and Pompeckj's illustrations confirm Whittard's assertion of the identity of the two genera. Although Brongniart's species has been reported from the Ordovician rocks of the Landeyran Valley on a number of occasions it has not been confirmed, and the genus is represented there by at least two new species.

Neseuretus antetristani sp. nov.

(Pl. 13, figs. 1–9)

DIAGNOSIS. Large species of *Neseuretus* with trapezoidal glabellar outline, the straight sides moderately convergent forwards. Three pairs glabellar furrows present but only weakly developed, especially on external moulds. Large paraglabellar areas poorly defined. Eyes small, opposite first glabellar lobes. Ocular ridges strongly developed, slightly convex forwards. Anterior area large, inclined forwards, its posterior half slightly convex and posterior half slightly concave dorsally. Outer parts of anterior area indented anterolaterally by pair large notches, possibly ends of anterior border furrow. Rostral suture in supramarginal position. Large pygidium has nine or ten axial rings and about seven pairs ribs.

HOLOTYPE. Brit. Mus. (Nat. Hist.) In.57475 (Pl. 13, figs. 3–5).

PARATYPES. In.56682 (Pl. 13, fig. 8) ; In.56857 ; In.57473 (Pl. 13, figs. 2, 6, 7) ; In.57474 (Pl. 13, fig. 9) ; In.57476 ; In.57478 (Pl. 13, fig. 1) ; It.274.

LOCALITIES AND HORIZON. All the known specimens are from the south-eastern side of the Landeyran Valley where the species occurs only in the Couches du Landeyran supérieures. The holotype is from $\lambda 17$, and other localities are $\lambda 16$ and $\lambda 20$.

DESCRIPTION. The cranidium is subtriangular in plan, one and a half times as broad as long, and strongly convex both longitudinally and transversely, with its dorsal surface steeply declined frontally. The glabella is convex, as broad as long, generally trapezoidal in outline, and narrows forwards noticeably so that the frontal breadth is half the basal breadth. The sides of the glabella are almost straight or gently convex outwards. One specimen (Pl. 13, fig. 9), preserved as an internal mould, shows a slight median carination of the glabella, which may be due to crushing. There are three pairs of glabellar lobes, declining in size from back to front of the glabella and separated by shallow glabellar furrows which are discernible in their entirety only on the internal mould. The centre of the glabella is occupied by a smooth median band, one-third of the glabellar breadth. The third glabellar lobes are the largest and expand in size laterally so that at the axial furrows they occupy two-fifths of the length of the glabella. The third glabellar furrows are broad (*exsag.*) and shallow at their intersection with the axial furrows, but arch thence backwards and inwards, finally stopping short of the occipital furrow so as to leave a pair of unfurrowed " necks " whose breadth (*exsag.*) is about one-third the length (*exsag.*) of the third lobes, as far as can be judged. The second glabellar lobes are just over half the size of the third lobes and poorly defined, even on the internal mould. The second glabellar furrows are slightly curved, convex forwards, shallow and broad (*exsag.*) at the axial furrows but dying out rapidly, apparently so as to end in-line with the third furrows. The first glabellar lobes are almost indiscernible and smaller than the second lobes. Like the other pairs of glabellar lobes, their convexity is continuous with that of the remainder of the glabella, and they are delimited by very faint first glabellar furrows ; a single internal mould shows the left first furrow (the only one preserved) in what Whittard (1960 : 143) described as a " perched " position on the glabella, and not reaching the axial furrow. The frontal glabellar lobe is approximately rectangular in plan, and about three times as broad as long (*sag.*). In detail its outline is rather more complex, the anterior margin having a broad (*tr.*) median indentation, and the anterolateral portions of the lobe expanding a little. In juxtaposition with each of these last features there occurs a large, almost square depression, in the concave floor of which is a suggestion of a hypostomal pit, situated immediately outside the anterolateral margin of the frontal glabellar lobe (see Pl. 13, figs. 3, 4). The axial furrows are narrow grooves situated at the bottom of large, broad furrows which are V-shaped in cross-section, with the adaxial side the more steeply declined. They are continuous forwards as far as the first glabellar furrows, at which point they are indented by the adaxial ends of a pair of large ocular ridges, which cause them to be deflected inwards for a short distance before turning outwards again to reach the pair of anterolateral depressions already mentioned as possibly containing the hypostomal pits. The depressions mark the outer ends of a broad (*sag.*) preglabellar furrow which flexes backwards medially, coincident with the indentation of the frontal glabellar lobe, and is slightly deeper abaxially. The portion of the cranidium between this furrow and the cephalic margin, and bounded posterolaterally by the " anterior furrows ", has been called the " anterior area " by Whittard (1960 : 143), who suggested that it probably represented

the combined anterior border and preglabellar field. In this instance the posterior half of the anterior area is slightly convex dorsally, whilst the anterior half is gently concave, the whole being strongly arched transversely (see Pl. 13, fig. 4). A curious feature of the species is the presence of a pair of large, deep notches (see Pl. 13, figs. 4, 5) which indent only the abaxial parts of the anterior area well forwards and may represent the outer ends of a now semi-obsolete anterior border furrow. The holotype cranidium retains the rostral plate *in situ* and this specimen shows that the rostral suture occupies a supramarginal position frontally (see Pl. 13, figs. 3, 5). The anterior branches of the suture run in straight lines from the eyes, converging forwards until they cut the anterior furrows and the deep notches (? anterior border furrow) just described. They then turn sharply inwards to meet frontally and form a rostral suture which runs close to the cephalic margin at the sagittal line but always remains slightly above it (Pl. 13, fig. 5). The rostral plate has the anterior and posterior margins parallel and arched forwards, and the ventral surface is convex. The connective sutures are not preserved, and the hypostoma is not known. The occipital ring is large, its maximum length (*sag.*) about a quarter that of the glabella. Parallel-sided over almost the median two-thirds, the occipital ring becomes shorter abaxially and flexes forwards slightly to form a pair of well-developed occipital lobes. The occipital furrow is shallow for most of its length (*tr.*) but deepens near the axial furrows, though it is not clear whether apodemes are present. The pleuroccipital furrow is deep, broad, well defined, subquadrate in cross-section, and almost straight transversely. The single outer end of this furrow preserved on the holotype suggests a slight curvature backwards, but this is probably due to crushing and one of the paratypes (Pl. 13, fig. 8) shows the pleuroccipital furrow curving forwards abaxially. The pleuroccipital segment is narrow (*exsag.*) immediately outside the axial furrows but quickly widens, particularly beyond the fulcra. The palpebral lobes are small, situated relatively far forwards, opposite the first glabellar lobes. They mark the outer ends of a pair of strongly-developed ocular ridges which curve outwards and slightly backwards from the axial furrows opposite the posterior half of the frontal glabellar lobe. The anterior portions of the fixigenae are small and decline steeply forwards, whilst the posterior portions are conspicuously large with their outer halves turned down sharply. The holotype exhibits a pair of large, quadrant-shaped paraglabellar areas, faintly defined by furrows which meet the axial furrows slightly behind the line of the third glabellar furrows and then curve outwards and backwards towards the pleuroccipital furrow. The posterior branches of the facial suture curve evenly and strongly back from the eyes to meet the genal angles.

The thorax, though incompletely known, comprises thirteen segments and is of the type characteristic for the genus. The axis is well defined by broad axial furrows and stands higher than the side-lobes. Each axial ring is transversely straight over its median half but turns forwards abaxially to form a pair of large axial lobes. The pleurae are parallelsided and transversely straight as far as the fulcra, beyond which they curve forwards and end in tips which are broadly rounded for the most part but angular posterolaterally. Each pleura carries a pleural furrow which commences at the anterior margin immediately outside the axial furrow. At first the

furrow is deep and narrow (*exsag.*), runs outwards and only slightly backwards until beyond the fulcrum, when it curves forwards gently, becomes broader and dies out towards the pleural tip. The anterolateral part of each pleura is slightly depressed so as to form a large articulating facet.

The pygidium is strongly convex, its axis declined backwards steeply and the side-lobes curved and sharply downturned laterally. The axis stands higher than the side-lobes and its straight sides converge backwards at about 30°. The largest pygidium has nine well-defined axial rings and a trace of a tenth, in addition to the articulating half-ring. The first two axial rings flex forwards near the axial furrows but the remainder are transversely straight, separated by uniformly and moderately deep ring furrows. The axial tip is small but distinct, followed by a rounded post-axial ridge extending to the tip of the pygidium. Each side-lobe has an anterior half-rib and, in the best-preserved specimen, seven well-defined ribs which curve backwards more strongly from first to seventh until the hindmost are only slightly divergent posteriorly. The pleural furrows separating the ribs run from the axial furrows and become shallower abaxially, but they can be traced to the pygidial margin. Each rib carries an interpleural furrow which is developed over its abaxial half and becomes fainter near the margin. A small pygidium from the type-locality has only seven axial rings and four or five ribs, but is believed to belong to the same species.

All the type-material is preserved as limonitic internal and external moulds and little remains of the surface ornamentation. Part of the right fixigena of the holotype exhibits evenly-distributed fine granulation, and similar ornamentation occurs on the surface of one paratype pygidium.

Discussion. For convenience the species of *Neseuretus* are discussed together after the description of *N. arenosus* sp. nov.

Neseuretus arenosus sp. nov.

(Pl. 14, figs. 1, 4, 5, 7–9, 11)

Diagnosis. Species of *Neseuretus* with short (*sag.*), broad glabella and three pairs glabellar lobes, those of first pair poorly defined. Frontal glabellar lobe broad (*tr.*) with anterior margin slightly concave medially. Anterior area relatively short (*sag.*), moderately declined forwards, its dorsal surface uniformly and gently convex and unfurrowed. Eyes opposite first pair and most of second pair glabellar lobes. Frontal parts of fixigenae broad. Pygidium with six axial rings, and five or six pleural ribs plus anterior half-ribs.

Holotype. Brit. Mus. (Nat. Hist.) In.57754 (Pl. 14, figs. 7, 9, 11).

Paratypes. In.57453 ; In.57751 (Pl. 14, figs. 1, 4, 8) ; In.57752 (Pl. 14, fig. 5).

Localities and horizons. The holotype and two of the paratypes are from the Couches du Foulon at locality λ7, on the north-western side of the Landeyran Valley almost 500 metres south-west of Upper Bridge. The remaining paratype was

found in a loose nodule weathered from, presumably, the Couches du Landeyran inférieures at a point about 400 metres north-east of l'Escougoussou.

Description. The exoskeleton is known only from isolated cranidia and pygidia. The cranidium is moderately convex, both transversely and longitudinally, with a projected length just over three-fifths of the projected breadth. The glabella is broader than long in the ratio 5 : 4, bounded by narrow axial furrows which are straight and slightly convergent forwards over the hindmost two-thirds of their length, becoming curved and slightly more convergent frontally. There are three unequal pairs of glabellar lobes, their dorsal convexity continuous with that of the median body of the glabella. The third glabellar lobes are the largest, subtriangular in plan with rounded margins, and connected to the median body by narrow (*exsag.*), slightly depressed " necks " ; posteriorly their convex margins invade the lateral thirds of the occipital ring. The third glabellar furrows are broad (*exsag.*), moderately deep, and curve inwards and moderately backwards ; each traverses about one-third of the glabellar breadth and broadens (*exsag.*) a little before ending almost level with the centre of the third glabellar lobes. The second glabellar lobes are relatively large, parallelsided, only slightly shorter (*exsag.*) than the third lobes, and end in tips which are gently rounded abaxially. The second glabellar furrows are parallel to those of the third pair and end longitudinally in-line with them, but are of uniform breadth (*exsag.*) adaxially. The first glabellar lobes are the smallest, just over half the length (*exsag.*) of the second lobes, but they also are parallelsided, delimited anteriorly by poorly-defined first glabellar furrows. The inner ends of the latter appear to line up with those of the other glabellar furrows, but as far as can be judged from the coarsely granulated state of preservation, their outer ends do not quite attain the axial furrows. The frontal glabellar lobe is small, subtrapezoidal in plan with the lateral margins strongly convergent forwards to broadly rounded anterolateral angles ; it is about five times as broad (*tr.*) as long, and the anterior margin is transversely almost straight, with a suggestion of being concave medially. The frontal margin of the cranidium is convex forwards and broadly rounded in plan. The anterior area (see Whittard 1960 : 143) is relatively short (*sag.*), between one quarter and one fifth of the projected median length of the cephalon, as well as broad (*tr.*), extending laterally until level with the hindmost parts of the axial furrows. Consequently the cranidial outline lacks the almost pointed, triangular appearance found in so many other species of the genus. In transverse section the anterior area appears gently declined overall, its surface gently and evenly convex. The anterior furrows forming the lateral boundaries of the anterior area are broad and shallow, markedly divergent forwards from the frontal ends of the axial furrows, the junction of the two marking the site of a pair of faint hypostomal pits. The occipital ring has a median length (*sag.*) one-quarter of that of the glabella. It is parallelsided over its median third but becomes narrower (*exsag.*) abaxially and curves forwards to form a pair of occipital lobes. The median third of the occipital furrow is transversely straight and shallow but the outer portions are slightly deeper, flexing gently backwards and then forwards again around the basal glabellar lobes. The eyes are

known only from the palpebral lobes, which are moderately convex in plan, converge forwards, and have almost flat dorsal surfaces. There are no visible palpebral furrows and only slight traces of ocular ridges running from the front of the palpebral lobes towards the frontal glabellar lobe. The anterior ends of the palpebral lobes are level with the first glabellar furrows, and the lobes terminate opposite the posterior half of the second glabellar lobes. The anterior branches of the facial suture are slightly more convergent forwards than the axial furrows, and cut the cephalic margin level with the outer ends of the basal glabellar lobes. The distance from the outer edge of each palpebral lobe to the axial furrow is about half the glabellar breadth measured across the second glabellar furrows, so that the frontal parts of the fixigenae appear relatively large and broad. The inner halves of the fixigenae are only moderately declined but the abaxial portions curve downwards strongly. In plan the posterior parts of the fixigenae appear almost quadrant-shaped and the posterior branches of the facial suture curve evenly and strongly backwards from the eyes. The pleuroccipital furrow is uniformly deep and broad (*exsag.*), transversely straight as far as the fulcra but then curves gently forwards. The pleuroccipital segment is parallelsided as far as the fulcra but becomes slightly wider (*exsag.*) towards the incompletely-known genal angles.

The pygidium is strongly convex transversely, with the dorsal surface of the axis steeply declined posteriorly. The outline is of the " taut bow " type, ending in a bluntly-pointed tip, with the length three-quarters of the projected breadth. The axis has a frontal breadth slightly less than half that of the pygidium, and its straight sides converge backwards at between thirty and thirty-five degrees towards the convex terminal piece. The axial furrows die out near the axial tip and there is a broad (*tr.*) postaxial ridge. In addition to the articulating half-ring there are six axial rings, the first three of which are slightly convex forwards and the remainder transversely straight. They are separated by ring furrows which are broad (*sag.*) medially but become narrower and shallower towards the axial furrows. The side-lobes carry, in addition to the anterior half-rib, five pairs of well-defined ribs and traces of a sixth pair. The pleural furrows separating the ribs are deep and narrow (*exsag.*), and all curve backwards, at first moderately and then more strongly, from the axial furrows to intersect the lateral margins. The outermost parts of the furrows, possibly coinciding with the limits of the pygidial doublure, are notably shallower, and the pairs of furrows become more strongly directed backwards from the first to sixth, until those of the last pair are subparallel. The interpleural furrows are only faintly impressed between the axial furrows and the fulcra, but their outermost portions are more deeply incised except near the pygidial margin, where they again become fainter. The pleural furrows divide the pygidial pleurae into anterior and posterior bands of which the former are conspicuously the narrower (*exsag.*). The anterolateral portions of the first pleura are strongly deflected ventrally to form a pair of large facets.

The Couches du Landeyran supérieures have yielded a few specimens of a small form of *Neseuretus*, for example at locality $\lambda 2$, in the lowest strata of this subdivision, and at localities $\lambda 16$, $\lambda 17$ and $\lambda 22$. At first it was suspected that these represented

nothing more than immature individuals of *Neseuretus antetristani*, but the suggestion has been discounted for a number of reasons : (i) the surface of the test is covered with fine granules ; (ii) the pleural furrows of the pygidium are better defined abaxially than in *N. antetristani* ; (iii) no intermediate stages have yet been found. Most important of all, one of the small cephala, In. 57755, retains part of the rostral plate and it can be seen that the frontal portion of the facial suture is submarginal, and not supramarginal as in *N. antetristani*. The specimens agree better with *Neseuretus arenosus* in the rather squat glabellar outline and shortness of the anterior border, and the fact that the latter appears more steeply upturned probably results from preservation in an argillaceous matrix. Two small pygidia from the Couches du Landeyran supérieures, though indifferently preserved, agree fairly well with that of *N. arenosus*. In the absence of good confirmatory evidence, all these specimens are listed in the present paper as *Neseuretus* cf. *arenosus*.

Discussion. The oft-quoted species *Neseuretus tristani* was described by Brongniart (1822 : 12, pl. 1, figs. *2a–k*) from the Schistes à Calymènes (mostly Upper Llanvirn Series) of the Cotentin Peninsula, western Normandy. Photographs of the type material have been published by Pompeckj (1903) and it is clear that the species is quite distinct from any yet found in the Montagne Noire. The glabellar outline of *N. tristani* is more rounded frontally and less convergent than that of *N. antetristani*, with better defined glabellar furrows. In *N. tristani* the paraglabellar areas are well developed and depressed below the level of the fixigenae, and consequently the posterior portions of the axial furrows appear less sharply defined than those of *N. antetristani*. In addition the anterior area of the Cotentin species is longer and more convex forwards than that of *N. antetristani*, whilst the rostral suture occupies a slightly inframarginal position. *Neseuretus arenosus*, although possessing well-defined glabellar furrows, is easily distinguished from species such as *N. tristani* by its squatter glabellar outline and shorter, only slightly convex, anterior area.

Whittard (1960 : 138–151) has described or redescribed several species of *Neseuretus* from the Shelve Inlier of West Shropshire, the majority of them occurring in the Arenig Series. All these species have deeply incised glabellar furrows and in most cases the anterior area is both longer and more sharply defined than in *Neseuretus antetristani*, but one of the paratypes of *N. brevisulcus* Whittard (1960, pl. 19, fig. 13) is of particular interest in exhibiting a pair of anterolateral expansions of the frontal glabellar lobe, separated by a median indentation, features reminiscent of the French species.

The only species of *Neseuretus* illustrated previously from the Ordovician rocks of the Montagne Noire was described by Thoral (1935*a* : 277, pl. 19, figs. 4*a*, *b*) as *Calymmene* [*sic*] (*Synhomalonotus*) *bergeroni*. Thoral's species was founded on material said to be from both the Tremadoc and Arenig Series, particularly in the St. Chinian and Prades-sur-Vernazobres districts ; the single specimen figured by Thoral, and now in the Bergeron Collection at the Sorbonne, is chosen here as lectotype. The glabellar outline of this apparently small species is reminiscent of that in *Neseuretus arenosus*, but the foremost part of the cephalon is markedly different,

consisting of a low, sharply upturned brim separated from the frontal glabellar lobe by a deep, almost transversely straight furrow. The pygidium of *N. bergeroni* is fairly distinct, having side-lobes with only the first two pairs of ribs clearly defined. No specimens undoubtedly referable to *Neseuretus bergeroni* have yet been found in the Landeyran Valley district and the small specimens of *Neseuretus* noted earlier in this account as *N.* cf. *arenosus* have a distinctively longer anterior area and better segmented pygidium than Thoral's species.

In describing *Calymene* (*Synhomalonotus*) *attenuata* from the Ordovician of Morocco, Gigout (1951 : 289, pl. 3, figs. 6, 7) stated that the species appeared to be present in the Montagne Noire, in the shales of Cabrières and in the sandstones above the Grès à Lingules. He claimed that the French material (in collections made by Thoral) had dimensions and glabella similar to those of *C.* (*S.*) *attenuata* but that the " bourrelet " (presumably corresponding to the anterior area) was raised up without being prolonged into a rostrum, a difference which he considered might be due to imperfect preservation. Monsieur J. Destombes has kindly supplied me with a photograph of Gigout's holotype and has given me a topotype cranidium which is now figured for comparison (Pl. 14, figs. 2, 6, 12). Both show that *C.* (*S.*) *attenuata* undoubtedly belongs to *Neseuretus* and I consider it to be specifically distinct from the specimens from above the Grès à Lingules, which are now described as *Neseuretus arenosus* sp. nov. The glabella of *N. arenosus* is proportionately shorter and less convergent forwards than that of *N. attenuatus*, and the frontal glabellar lobe is both shorter and broader, with no " step " in the glabellar outline at the first glabellar furrows. The anterior area of *N. attenuatus* is longer, narrower and more strongly arched transversely than that of *N. arenosus*, and whilst such differences could possibly be accounted for by vagaries of preservation (though this is considered unlikely), the anterior area of the Moroccan species is convex over its posterior half, becoming concave towards the raised cephalic margin, features contrasting markedly with the short, uniformly convex anterior area of *N. arenosus*. The age of *N. attenuatus* was stated originally by Gigout to be " Llandeilo " (in fact, upper Llanvirn), but in a more recent revision of the appropriate stratigraphy the species is recorded from the Lower Llanvirn Series (Gigout 1956 : 2740), that is to say an horizon later than that of *N. arenosus* in the Montagne Noire.

A species of *Neseuretus* resembling *N. arenosus* in some respects is that described originally as *Calymene* (*Synhomalonatus*) [*sic*] *convexia* from the Llanvirn Series of south-western China (Sheng 1958 : 201, pl. 7, fig. 6). Sheng's illustration makes it difficult to discern the glabellar outline of *Neseuretus convexius*, though it seems broadly comparable to that of *N. arenosus*, but both species share a relatively short (*sag.*) anterior border and fixigenae which are noticeably broad frontally. The test of *N. convexius*, like that of specimens of *N.* cf. *arenosus* from an argillaceous matrix in the Landeyran Valley, is finely granulated, but the eyes of the Chinese species are sited opposite the first glabellar lobes, or even part of the frontal glabellar lobe, that is to say conspicuously farther forwards than in the French form. *Neseuretus tungtzuensis* Sheng (1958 : 200, pl. 7, figs. 5a–c), from a horizon similar to that of *N. convexia* was said by Sheng to be closely related to the latter species, but appears

to be quite distinct from both it and *N. arenosus* on account of the narrower, straight-sided, less convergent glabellar outline and much longer anterior area.

Family **EOHOMALONOTIDAE** Hupé 1955

Genus ***PLATYCORYPHE*** Foerste 1910

Platycoryphe convergens sp. nov.

(Pl. 14, figs. 3, 10, 13)

Diagnosis. Species of *Platycoryphe* with sub-trapezoidal glabellar outline, narrowing forwards slightly. No distinct glabellar furrows but position of glabellar lobes indicated by three pairs of indentations along sides of glabella. Eyes situated opposite first glabellar lobes. Anterior border short, inclined.

Holotype. Brit. Mus. (Nat. Hist.) In. 57756.

Locality and horizon. The only known specimen is from locality λ19, on the hillside south-east of Route D. 136, near the southern end of the Landeyran Valley. The horizon is in the Couches du Landeyran supérieures.

Description. Cranidium slightly less than twice as broad as long. The glabella is only moderately convex, both longitudinally and transversely, but stands noticeably higher than the fixigenae. In outline it is sub-trapezoidal, with frontal breadth slightly more than half the basal breadth. There are no distinct glabellar lobes and furrows, but their position is indicated by three pairs of small constrictions of the sides of the glabella. Those representing the third glabellar furrows are situated about three-eighths of the distance from the back to the front of the glabella, but the first and second furrows are slightly closer together, marking first and second pairs of glabellar lobes, each equal to about one-quarter of the length of the glabella. The indentations become progressively less marked from back to front of the glabella, whilst the first glabellar lobes are slightly more convex than those of the other pairs. There is a faint suggestion of a median carination of the glabella, and although such a feature is not uncommon in homalonotid trilobites its presence here may well be due to crushing, which is particularly visible on the right side of the glabella. The axial furrows are deep and well defined, apparently without constrictions corresponding to the glabellar furrows. This is so in the case of the left axial furrow, and the flexures of the right furrow are probably due to mechanical causes. There is no definite evidence of hypostomal pits. The frontal glabellar lobe is twice as broad as long, gently convex frontally and rounded anterolaterally. At either side it is strongly defined by the axial furrows, but the latter diminish forwards and form only a shallow groove antero-medially, representing the preglabellar furrow. The anterior border is short and thin, with a sharp dorsal edge, and strongly upturned with a slight suggestion of thickening at and near the sagittal line. There is no anterior border furrow or discrete preglabellar field, but the area immediately in front of the glabella is slightly flattened, and broadens laterally towards the axial furrows. This can be seen on the right side of the holotype, but the left side of the same specimen appears

to show a short (*tr.*) extension of the fixigena in front of the frontal glabellar lobe. The occipital ring is longest (*sag.*) medially, where it is equal to almost one-sixth of the glabellar length, narrowing (*exsag.*) laterally to form a pair of small occipital lobes. The occipital furrow is well defined transversely straight and deepens laterally. The pleuroccipital segment is narrow (*exsag.*) proximally but broadens a little towards the genal angles. The pleuroccipital furrow is transversely straight, narrow and deep outside the axial furrows, becomes wider and shallower abaxially, its outer ends incompletely preserved. The eyes and palpebral lobes are not preserved, but were sited well forwards, opposite the first glabellar lobes and only a little way out from the axial furrows. The anterior parts of the fixigenae are thus relatively short and narrow, bounded by the anterior branches of the facial suture which run forwards from the eye, parallel to the axial furrows, to cut the anterior border and curve inwards, passing below the top of the border. The posterior parts of the fixigenae are long (*exsag.*), convex, steeply declined laterally, and the posterior branches of the facial suture curve backwards, gently at first and then more strongly, from the eyes to cut the cephalic margin in what appears to be a gonatoparian position, though the genal angles are incomplete. The librigenae and the remainder of the exoskeleton are not preserved. The surface of the test appears to be generally smooth, as far as can be judged, and the apparent granulation of the internal mould is due to the state of preservation.

Discussion. The new species belongs to a group of trilobites which had a long history and wide distribution during Ordovician times, though they have previously been unrecorded from strata below the Llanvirn Series. Whittington's (1965) illustrations show that all the known North American species have well-defined glabellar furrows, but in some individuals described from the Caradoc Series of South Shropshire (Dean 1961 : 344) they may become diminished. Certain specimens of *Platycoryphe vulcani* (Murchison), redescribed by Whittard (1961 : 164) from the Llanvirn Series of West Shropshire, have a smooth glabella, reminiscent of that of *Brongniartella*, whilst others of the same species have easily visible glabellar furrows.

Paraglabellar areas do not appear to be developed in the Landeyran Valley species. Such structures have been described in *Platycoryphe dentata* Dean (1961 : 340) from South Shropshire, as well as by Whittington (1965) in the type-species *P. christyi* (Hall). On the other hand paraglabellar areas are visible on certain specimens of *Platycoryphe vulcani* (see Whittard 1961, pl. 22, figs. 8, 12) though not in others, and were not mentioned in the description of the species. A similar state of affairs exists for *Brongniartella*, only occasional specimens of which exhibit well-defined paraglabellar areas. The steeply upturned nature of the anterior border in *Platycoryphe convergens* is possibly mechanical in origin. At all events it contrasts markedly with the rather flattened, scoop-like structure of *Platycoryphe vulcani*, and the thickened, though upturned, border of *P. christyi*. In *P. vulcani* the eyes are sited opposite the second, and part of the first, glabellar lobes, and in the other described species opposite the second lobes, whereas those of *P. convergens* are placed relatively far forwards, in line with the first glabellar lobes. The anterior margin of the frontal

glabellar lobe is more rounded in plan and less well defined than in any other described species of the genus.

A trilobite of homalonotid type was described by Kobayashi (1937 : 490, pl. 3, figs. 15–17) as *Homalonotus* (*Brongniartella?*) *bistrami* Hoeck, from the Ordovician (?Lower) of Bolivia. Harrington & Leanza (1957 : 224) have pointed out that the pygidium of this form is unlikely to be that of a true *Brongniartella*, and one might add that the associated cephala illustrated by Kobayashi bear some resemblance to that of *Platycoryphe*, although the material is distorted and difficult to evaluate.

Family **ASAPHIDAE** Burmeister 1843

Subfamily **ASAPHINAE** Burmeister 1843

Genus ***BASILIELLA*** Kobayashi 1934

Basiliella mediterranea sp. nov.

(Pl. 16, fig. 5 ; Pl. 17, figs. 1, 3, 4, 8, 11–13)

Diagnosis. Glabella moderately convex, broadest basally, narrowing medially but expanding to well-rounded frontal lobe. One pair large, triangular glabellar lobes present, their anterolateral "angles" slightly depressed. Eyes placed opposite centre of glabella. Facial suture dorsal-intramarginal with anterior branches moderately divergent forwards, meeting frontally at obtuse angle. Preglabellar field narrow (*sag.*), slightly convex. Anterior border forms narrow rim. Small median tubercle sited in front of occipital furrow. Librigenal spines long, slim. Hypostoma with posterior border deeply notched. Thorax of eight segments. Pygidium semicircular in outline with concave border ; nine or ten axial rings and seven pleural ribs present.

Holotype. Brit. Mus. (Nat. Hist.) It.399 (Pl. 17, figs. 1, 4).

Paratypes. In.56847 (Pl. 17, fig. 3) ; In.56856 (Pl. 17, figs. 11, 13 ; It.257 (Pl. 16, fig. 5 ; Pl. 17, fig. 8) ; It.260 (Pl. 17, fig. 12).

Localities and horizons. Most of the type-material of this uncommon species is from the Couches du Landeyran supérieures cropping out along the eastern side of the Landeyran Valley. The holotype was obtained from locality λ21 and two of the paratypes from λ8 and λ17, but the species was found also at λ19. *B. mediterranea* occurs, though rarely, in the Couches du Landeyran inférieures and one of the paratypes is from locality λ31 at the hillside section 240 metres south-west of Le Foulon.

Description. The glabella is moderately convex both longitudinally and transversely, and has a basal breadth about five-sixths of the median length. It is well rounded frontally but narrows opposite its mid-point to about five-sixths the frontal breadth, resulting in a waist-like appearance ; the glabella then expands again, reaching a maximum at its base, where the breadth is one and a quarter times that of the frontal lobe. There is a single pair of large, basal, glabellar lobes, triangular in

plan, with their anterolateral portions depressed slightly below the level of the adjacent glabella. The glabellar furrows are straight and broad (*tr.*), run sharply backwards adaxially from the axial furrows at points opposite the centre of the glabella, and end abruptly so as to leave a narrow, unfurrowed, median band. A slight flexure affects the left, but not the right, basal glabellar furrow of the holotype and is apparently the result of crushing. The axial furrows are broad, moderately deep, become shallower at their mid-points, opposite the outer ends of the basal glabellar furrows, and fuse frontally with the preglabellar furrow. There is a gently convex preglabellar field, narrow (*sag.*) medially but broader abaxially and merges with the frontal portions of the fixigenae. It is bounded frontally by a broad (*sag.*), shallow, anterior border furrow, in front of which is developed a narrow, rim-like, anterior border. The occipital furrow is only moderately impressed medially, then becomes deeper, possibly due to the presence of a pair of apodemes, and finally markedly shallower at its extremities. The occipital ring is parallelsided with only a suggestion of a pair of occipital lobes ; the latter scarcely extend level with the outer margins of the basal glabellar lobes and are poorly differentiated from them. Both the occipital furrow and ring of the holotype appear to be flexed forwards abaxially but this has probably been exaggerated by crushing. The pleuroccipital furrow is broad (*exsag.*), moderately deep, curves backwards a little abaxially, whilst the pleuroccipital segment expands only slightly in size towards the genal angles. The palpebral lobes, although incompletely known, are moderately convex, their dorsal surfaces gently declined adaxially, sited a little behind centre with reference to the glabella, and immediately outside the axial furrows. One of the paratypes retains the left librigena and although this is displaced it can be seen to end in a long, slim, curved, librigenal spine which must have extended backwards as far as the anterior half of the pygidium. The eye is reniform, convex, and the visual surface is holochroal, though only a fragment is preserved. No distinct eye-platform is developed and the surface of the librigena declines steeply from the eye to a broad, smooth furrow, beyond which is a raised, narrow, lateral border. The surface of the cephalic margin and doublure at this point is ornamented with closely-grouped, subparallel terrace-lines. The anterior branches of the facial suture curve forwards and outwards from the eyes almost to the anterior border furrow ; there they turn through about a right-angle, cut the anterior border obliquely and curve smoothly inwards. Near the sagittal line they turn forwards slightly before meeting at an obtuse angle, so that on the cranidium the median part of the anterior border is bluntly pointed. The posterior branches curve backwards abaxially, at first gently and then more sharply, probably cutting the posterior cephalic margin outside the fulcra. Apart from the terrace-lines of the cephalic margin and doublure already mentioned, the test is smooth.

One of the paratypes (Pl. 16, fig. 5 ; Pl. 17, fig. 8) retains the hypostoma almost in place. Although the anterior portion is incomplete, the entire hypostoma is estimated to have had a maximum breadth almost equal to the length. The frontal margin appears to have been rounded in plan and no trace of an anterior border has been found. The lateral margins are rounded and the overall breadth of the hypostoma increases from front to back for about three-quarters of the length, coinciding

with a progressive broadening of the lateral border. The latter is flattened and continues backwards as a pair of large, posterior wings, separated by a median notch whose depth is estimated as about one-eighth of the entire length of the hypostoma. The median body is large, convex, ovoid in plan and narrows posteriorly. It is bounded laterally by a broad, deep furrow which continues posteriorly so as to delimit the posterior border, and runs transversely a short distance in front of the median notch. The median body is traversed by a curved median furrow, concave forwards and shallowest medially. The two lobes so formed are markedly unequal, the median length of the anterior being about six times that of the posterior lobe. The latter is subcrescentic in plan, expanding a little abaxially where the antero-lateral halves show traces of a pair of maculae.

An isolated hypostoma, It.269 (Pl. 17, fig. 9) from locality $\lambda 32$, is referred tentatively to *B. mediterranea* and resembles that of paratype It.257 in many respects, but the median body has a slightly larger posterior lobe and the posterior border is indented by a narrower median notch. In this last feature the specimen resembles another hypostoma, In.57742 (Pl. 17, fig. 6), here named only *Basiliella* sp., from locality $\lambda 17$, but the latter has an almost circular anterior lobe. Yet another hypostoma referred to *Basiliella*, In.56844 (Pl. 17, fig. 2) also from $\lambda 17$, is larger than the other specimens and differs from them in having an extremely broad, deep, median notch in the posterior margin, a less well-defined posterior lobe, and more pointed posterior wings.

The thorax comprises eight segments and the axis, which stands well above the side-lobes, occupies a little less than one-third of the total projected breadth. The axial rings are transversely rectangular in plan, bounded laterally by deep, broad, axial furrows. The pleurae are parallelsided and transversely straight for half their length (*tr.*) but then turn backwards slightly to the pleural tips which are obliquely truncated and form short points directed posterolaterally. Each pleura carries a pleural furrow which begins just outside the axial furrow and is shallow at first, becomes deeper as it traverses the fulcrum but shallows again and dies out mid-way between the fulcrum and the pleural tip. The anterior band has a narrow (*exsag.*), ridge-like appearance at and near the fulcrum owing to the development of a large, articulating facet anterolaterally.

The pygidium is slightly convex, one and a half times as broad as long. The anterior margin arches gently backwards and outwards from the axis to well-rounded anterolateral angles, behind which the lateral margins run backwards and inwards so that the outline forms a broad, smooth, parabolic curve. The axis is narrow, its frontal breadth just less than a quarter of that of the pygidium and its sides slightly convergent backwards, bounded by straight, deep axial furrows. The available material shows nine or ten transversely straight axial rings, followed by a narrow, blunt, almost smooth tip. The latter is separated from the posterior margin of the pygidium by a concave border which is narrow (*sag.*) posteriorly but widens antero-laterally before becoming slightly narrower near the frontal margin of the pygidium, where a pair of facets is situated. There is no postaxial ridge. The side-lobes curve gently downwards from the axial furrows and carry, in addition to the anterior half-

rib, seven pairs of ribs, the seventh pair being less distinct than the others, followed by a small, unfurrowed area on either side of the axial tip. The pleural furrows are straight for most of their length (*tr.*), but curve backwards slightly just before attaining the inner side of the lateral border, where they end. The ribs are a little wider at their outer ends, become progressively more strongly directed backwards from front to back of the pygidium, and are flattened dorsally, with only faint traces of interpleural furrows.

Discussion. *Basiliella* was founded by Kobayashi (1934 : 469) on *Asaphus barrandi* Hall 1851 (sometimes misquoted as *A. barrandei* sic) and used by him for certain South Korean trilobites. Since then specimens of Upper Tremadoc age have been assigned to the genus (Harrington 1938 : 257 ; Harrington & Leanza 1957 : 145). All these species have a conspicuous axial ridge across the preglabellar field, a feature which is absent from the type-species as illustrated by Hall (1851 : 210) and Raymond (1914 : 261), and there must be some doubt as to their true generic position. Jaanusson (*in* Moore 1959 : O 336) has redefined *Basiliella*, regarding it as a subgenus of *Basilicus*, and has given new line-drawings of the type-species of both genera. He shows the cephalon of *Basiliella* with longer librigenal spines, more divergent anterior branches of the facial suture, and less pointed posterior wings on the hypostoma than *Basilicus*. He emphasizes, however, the short, broad, almost semicircular pygidium of *Basiliella*, a feature which Kobayashi (1934 : 469) had regarded as being of generic significance, contrasting markedly with the long, subtriangular, better-segmented pygidium of *Basilicus*. *Basiliella mediterranea* agrees in all essentials with *B. barrandi* (Hall), but may be distinguished by the following features : (i) the anterior branches of the facial suture are less divergent forwards ; (ii) the basal glabellar lobes are larger and better defined, so that the posterior half of the glabella is notably wider ; (iii) the occipital furrow is deeper and curved, whilst the median tubercle immediately in front of it is smaller ; (iv) the librigenal spines are slimmer and longer. Jaanusson's restoration of the cranidium of *Basiliella barrandi* shows the frontal margin as an unbroken curve, but Raymond's figures illustrate clearly the intramarginal facial suture, with the two branches curving forwards slightly near the sagittal line to meet at an obtuse angle. A similar feature is seen in *B. mediterranea*, though the anterior border is probably rather narrower (*sag.*). The various illustrations of the pygidium of *B. barrandi* are somewhat contradictory, but there appear to be more pleural ribs than in the French species, though the number of axial rings seems at least roughly comparable. Hall's original material of *Basiliella* came from the Black River group of Wisconsin and is therefore considerably younger than the specimens from the Montagne Noire.

Subfamily **ISOTELINAE** Angelin 1854
Genus ***MEGISTASPIS*** Jaanusson 1956
Subgenus ***EKERASPIS*** Tjernvik 1956
Megistaspis (***Ekeraspis***) sp.

(Pl. 16, figs. 2, 9, 10)

Ekeraspis was first established by Tjernvik (1956 : 242) as a subgenus of *Plesio-*

megalaspis, but has since been claimed as a subgenus of *Megistaspis* by Jaanusson (*in* Moore 1959 : O 349), whose convention is followed here. According to Jaanusson, in *Megistaspis* the glabella is parallelsided or tapered, there is a concave cephalic border, and the " frontal area " occupies at least 25% of the length of the cranidium. The anterior branches of the facial suture of the type-species of *Megistaspis* and *Ekeraspis* differ markedly, those of the former diverging forwards only slightly before curving inwards and meeting well forwards at an acute angle. In *Ekeraspis* the anterior branches diverge forwards more strongly as far as the cephalic border, where they turn sharply inwards and meet frontally at an obtuse angle. A few cranidia, the largest with a median length of about 25 mm., from the Landeyran Valley–Le Foulon district exhibit all these features, and differ in only small respects from the type-species *M.* (*E.*) *armata* (Tjernvik 1956 : 242), described from the early Arenig Series of Sweden. The French specimens have slightly less divergent anterior branches of the facial suture, the poorly differentiated frontal glabellar lobe is broader, and the eyes are positioned a little farther forwards. The pygidium of *M.* (*E.*) *armata* is a distinctive structure with a broad, concave border which becomes still broader posteriorly and merges with a stout terminal spine. No comparable pygidium was found during the present collecting, but the pygidium of *Megalaspis filacovi* Munier-Chalmas & Bergeron (see Thoral 1935*a* : 226), from the Upper Tremadoc Series of the St. Chinian district, is of closely similar type, though smaller and generally with a longer, slimmer, terminal spine. Two small, slightly compressed pygidia (Pl. 15, figs. 5, 6, 8), each ending in a small spine, are provisionally assigned to *Ekeraspis*. The axis is narrow with traces of seven or eight axial rings, whilst the side-lobes carry at least five pairs of ribs which become fainter posteriorly. The border is smooth and broad but not concave, though this may have been obscured by compression. A more satisfactory determination must await the collection of further specimens.

A single, large hypostoma (see Pl. 16, fig. 11) from an unspecified horizon and locality in the Landeyran Valley almost certainly originated from the Couches du Landeyran. It bears a considerable resemblance to one figured by Thoral (1935*a*, pl. 25, fig. 2) as *Megalaspis* (?) sp., from the Upper Tremadoc or Lower Arenig of the St. Chinian district. Thoral considered such forms to be related to his species *Megalaspis* (?) *boehmi*, but the hypostoma of the latter, though generally similar (Thoral 1935*a*, pl. 27, fig. 4), differs from the present specimen in having the margins of the anterior lobe more strongly convergent backwards, so that the maculae are situated closer together. In the absence of additional material the specimen is referred merely to *Megistaspis* (s.l.).

Genus ***MEGALASPIDELLA*** Kobayashi 1937

Subgenus ***MEGALASPIDELLA*** Kobayashi 1937

1946. *Plesiomegalaspis* Thoral : 61.

Megalaspidella (***Megalaspidella***) sp.

(Pl. 16, fig. 12 ; Pl. 17, fig. 7)

According to Thoral (1946 : 70) *Paramegalaspis*, although closely resembling

Plesiomegalaspis, is always smaller and more convex, and has less well developed borders, whilst the pygidial axis is very indistinct. Future revision may well show these criteria to be insufficient for generic separation, but for the present I follow Jaanusson (*in* Moore 1959 : O 347, O 349) in regarding *Plesiomegalaspis* as a probable synonym of *Megalaspidella* sensu stricto and distinct from *Paramegalaspis*.

The type-species of *Plesiomegalaspis*, *P. graffi*, was described by Thoral (1946 : 61) from the Cabrières district, north-east of the Landeyran Valley, where it occurs commonly in association with *Niobella fourneti* (Thoral), raphiophorids and agnostids. Such an assemblage suggests that one might expect to find the genus in at least the Couches du Landeyran inférieures, but several large specimens of appropriate type which were collected proved too distorted for certain identification. A small cephalon preserved as an internal mould (Pl. 16, fig. 12) shares most essential features with *M. graffi* but has rather larger eyes than that form, though this may be due to its representing an earlier stage of development. The unthickened anterior border is certainly like that of Thoral's species, whilst both have the anterior branches of the facial suture diverging forwards more strongly than has a typical *Paramegalaspis*.

A large hypostoma (Pl. 17, fig. 7) from the Couches du Landeyran inférieures near Le Foulon has an elongated, elliptical median body, cut abaxially by the deep, outer ends of an otherwise shallow, transverse, median furrow. The centre of the posterior margin is marked by a short point, separated by small indentations from broad posterior wings which do not extend backwards beyond the median point. The hypostoma strongly resembles that of *Megalaspidella* [*Plesiomegalaspis*] *graffi* but is relatively narrower. One of Thoral's syntypes of the *forma typica* of his species (1946, pl. 12, fig. 1*a*) shows the posterior margin of the hypostoma with a small median notch, but the photographs of *M. graffi* var. *major* and *M. angustirachis* (Thoral 1946, pl. 7, fig. 1 and pl. 16, fig. 2) indicate a small, median point.

Genus ***PARAMEGALASPIS*** Thoral *in* Jaanusson 1956

1935*a*. *Paramegalaspis* Thoral : 238. *Nomen nudum.*

Paramegalaspis cf. ***frequens*** Thoral

(Pl. 18, figs. 1–3, 8, 10, 13)

1935*a*. *Paramegalaspis frequens* Thoral : 243.

The remains of asaphid trilobites are relatively common in the Couches du Landeyran. Unfortunately they are usually disarticulated and too distorted for certain identification, but the majority probably belong to *Paramegalaspis*. Much of the material assigned to this genus by Thoral was preserved as internal and external moulds in siliceous nodules, and a few similar examples have been found in the Landeyran Valley. A pygidium (Pl. 18, figs. 2, 10, 13) in a loose nodule from,

probably, the Couches du Landeyran inférieures, has traces of about eight axial rings and six pleural ribs, figures which are appropriate for *P. frequens*, but the anterior margin is straighter than that of the latter species and the lateral border is slightly less well defined.

An unfigured cranidium, In. 57738, from a loose nodule near locality λ17, is closely similar to that of *Paramegalaspis immarginata* Thoral (1935*a* : 248) but the eyes are sited a little farther forwards. Like *P. immarginata* this specimen has an almost obsolete anterior border, but a larger cranidium (Pl. 18, figs. 1, 3, 8) from the same vicinity is similar in most respects except that of the anterior border. The latter is more strongly developed and the frontal glabellar lobe and preglabellar field are better defined, such features being more appropriate to *Paramegalaspis frequens* or one of its varieties. A revision of *Paramegalaspis* is beyond the scope of the present paper, but one cannot rule out the possibility of variation within the various species, and allegedly diagnostic features might well be at least partly dependent on the size of the specimen. The genus was described from both the Tremadoc and Arenig Series by Thoral, so it might be expected to occur in the strata below the Couches du Landeyran. Such evidence is, in fact, scanty but a hypostoma (Pl. 18, fig. 9) from the Couches du Foulon agrees with Thoral's (1935*a* : 239) diagnosis of *Paramegalaspis*, though the median furrow is slightly deeper than stated by him.

Two small pygidia figured here (Pl. 18, figs. 11, 12) are typical of several collected from both the lower and upper subdivisions of the Couches du Landeyran. Although crushed to varying degrees they resemble the pygidium of *Paramegalaspis* in all essentials, whilst the broad, smooth border is similar to that of *P. frequens* var. *depressa* Thoral (1935*a* : 247).

Numerous immature specimens of *Paramegalaspis* were obtained from the Couches du Landeyran, and although most had suffered from the effects of weathering, a few fairly well-preserved examples were recovered, particularly at localities λ16 and λ30. The smallest (Pl. 17, fig. 5), which probably represents Meraspis Degree 3, has a cephalic length (*sag.*) and breadth of 1·6 mm. and 3·0 mm. (estimated) respectively. The area in front of the glabella is smooth and undivided, whilst the glabella is more convex and the eyes larger than in the adult. Slim librigenal spines extend at least level with the centre of the pygidium, which has a broad, smooth border and poorly differentiated ribs. Meraspis Degree 4 (Pl. 17, fig. 14) resembles Degree 3 in most respects, but has a slightly shorter transitory pygidium. In Meraspis Degree 6 (Pl. 17, fig. 15) the length and breadth of the cephalon are 2·1 mm. and 3·6 mm. (estimated) respectively, whilst the total length of the exoskeleton is about 4·8 mm. The eyes are still relatively large, and the librigenal spines are unusually long, extending a little beyond the tip of the pygidium. Pl. 17, fig. 10 probably represents Meraspis Degree 7, and the total length is about 7·1 mm. The eyes are smaller and the pygidial border is narrower than those of earlier growth stages. The librigenal spines, though not entirely preserved, give the impression of being notably shorter than those of Degree 6 described above, and there may have been some variation in their length.

Genus *HOEKASPIS* Kobayashi 1937

Hoekaspis? *quadrata* sp. nov.

(Pl. 19, figs. 1–10, 12)

Diagnosis. Glabella subrectangular, longer than broad, with frontal margin slightly convex. Anterior border well defined, broadens (*sag.*) a little medially, separated from glabella by deep furrow of even breadth. Occipital and pleuroccipital furrows deep, almost straight. Palpebral lobes unfurrowed, convex, sited well back, close to axial furrows, their length half that of glabella.

Holotype. Brit. Mus. (Nat. Hist.) It.428 (Pl. 19, figs. 1, 3, 5, 7–9).

Paratypes. It.429 (Pl. 19, figs. 2, 4, 6, 12) ; It.430 (Pl. 19, fig. 10).

Locality and horizon. Locality λ6 in the south-eastern bank of the river near the northern end of the Landeyran Valley. The horizon is low in the Couches du Landeyran inférieures.

Description. The species is represented by only three associated, slightly compressed cranidia, each moderately convex transversely with its dorsal surface gently declined forwards, except when distorted mechanically. The glabella is longitudinally subrectangular in outline with the corners rounded, whilst the frontal margin is slightly convex. The glabella of the holotype, the largest specimen, is about five-sixths as broad as long, but that of the smallest example is conspicuously narrower, with the breadth only three-fifths of the length, and may represent an earlier stage of development. There are no glabellar furrows and the unfurrowed glabella is bounded by straight, nearly parallel, axial furrows which are broad and deep for the most part but become shallower frontally, where a pair of hypostomal pits is situated on their inner margins, just behind the anterolateral angles of the glabella. The frontal part of the cranidium is formed by a well-developed anterior border with flattened dorsal surface and median breadth (*sag.*) about one-seventh of the length of the glabella, separated from the latter by a deep, parallel-sided furrow of similar breadth. The posterior margin of the anterior border is steeply bevelled and the front of the glabella is well defined but there is no development of a distinct, furrow-bounded, preglabellar field. The median two-thirds of the occipital ring are uniformly broad (*sag.*) but the ends are narrow and turn forwards slightly to form a pair of occipital lobes. The occipital furrow is deep and transversely straight except for the extremities which curve forwards around the posterolateral angles of the glabella. The pleuroccipital segment, though incompletely known, apparently broadens (*exsag.*) abaxially, and is delimited by a deep pleuroccipital furrow. The palpebral lobes are convex in plan and fairly large, their length (*exsag.*) half that of the glabella. They are placed just outside the axial furrows and end posteriorly a little in front of the line of the occipital furrow. Their dorsal surfaces decline gently towards the axial furrows. The anterior branches of the facial suture are straight and slightly divergent at first but then curve adaxially so as to cut the anterior border and meet frontally in a broad arc or at a very blunt point. The posterior

branches run outwards and gently back for more than half their length (*tr.*) but then turn more sharply back to the posterior margin, so that the hindmost portions of the fixigenae are small and subtriangular. The surface of the test is smooth.

DISCUSSION. *Hoekaspis* was founded by Kobayashi (1937 : 496) and has since been redefined by Harrington & Leanza (1957 : 176). The generic position of the scanty sample from the Landeyran Valley is by no means clear, but the species agrees with the definition of *Hoekaspis* in the following respects : (i) the glabella is almost rectangular in plan, bounded by broad axial furrows ; (ii) the anterior border is convex, set lower than the glabella and separated from it by a distinct furrow ; (iii) the facial suture is intramarginal. On the other hand, the occipital furrow, unlike that of other species of *Hoekaspis*, is well defined and the eyes are larger than in any other members of the genus, whilst the furrow separating the glabella and anterior border is unusually deep and broad (*sag.*), but this last feature may have been exaggerated by compression. No median tubercle has been found on the glabella of *H.? quadrata*, but this may be the result of poor preservation, and the same structure is not obvious in all of Harrington & Leanza's illustrations.

Subfamily **NIOBINAE** Jaanusson 1959

Genus ***NIOBELLA*** Reed 1931

In his original definition of *Niobella* Reed (1931 : 462–463) laid stress on the form of the hypostoma in separating the genus from *Niobe* sensu stricto, that of *Niobella* having a sub-pointed or rounded posterior margin. He regarded the pygidium as being virtually identical in both genera. Lake (1942 : 330), however, has questioned the significance of the hypostoma, demonstrating that the posterior hypostomal margin of *Niobe* (s.l.) underwent successive changes. More recently Tjernvik (1956 : 223, 228) has redescribed various members of both *Niobe* (including *N. frontalis* (Dalman) the type-species) and *Niobella* from the Lower Ordovician of Sweden. He has demonstrated that the pygidium gives a reliable means of separation, that of *Niobe* having ribs which are mostly rounded in cross-section, extending outwards beyond the inner margin of the doublure to end in tips which bulge abaxially, whilst the pygidium of *Niobella* has ribs which are well developed as far as the doublural margin and then merge into the flattened border. Tjernvik's illustrations suggest also that the eyes of *Niobe* are placed closer to the glabella, and that the lobation of the glabella is better defined than in *Niobella*. On the basis of these criteria most of, if not all, the species from the Montagne Noire hitherto assigned to *Niobe* should be transferred to *Niobella*.

Niobella fourneti (Thoral)

(Pl. 15, fig. 9)

1946. *Niobe fourneti* Thoral : 74–82, pl. 1 ; pl. 2, fig. 1 ; pl. 3 ; pl. 4, fig. 1 ; pl. 5, figs. 1*a*, *b*; pl. 6, figs. 3, 4 ; pl. 11, fig. 5 ; pl. 16, fig. 1.

A slightly compressed cranidium in an old collection from, presumably, the

Couches du Landeyran inférieures at or near Le Foulon, and preserved as an internal mould, agrees with Thoral's description of the species in all respects save that of size. *N. fourneti* was described from the " Schistes à Gateaux " of the Cabrières district, where the species is relatively abundant and generally attains large dimensions.

***Niobella* cf. *lignieresi* (Bergeron)**

(Pl. 15, figs. 2, 4)

1895. *Ogygia lignieresi* Bergeron : 476, pl. 5, fig. 4.
1935*a*. *Niobe lignieresi* (Bergeron) Thoral : 258, pl. 24, figs. 2–4 ; pl. 27, fig. 2.

The Couches du Landeyran inférieures in the northern part of the Landeyran Valley have yielded a number of fragments of *Niobella*, and two of the best preserved may be compared with *N. lignieresi*, though both are notably larger than the single specimen figured by Bergeron. A cranidium (Pl. 15, fig. 2) from locality $\lambda 4$ shows a pronounced, almost transverse depression just behind centre of the glabella, and although this has undoubtedly been exaggerated by crushing, the holotype (Bergeron 1895, pl. 5, fig. 4) shows traces of a similar structure. The conspicuous, anastomosing ridges forming a Bertillon pattern on the cranidium from the Landeyran Valley were not mentioned by Bergeron, but he pointed out, in describing the lack of glabellar lobation, that the test of the holotype was not preserved. The pygidium from locality $\lambda 5$ now figured has a relatively narrow axis with six well-defined axial rings and traces of another four, whilst the side-lobes have three sharply delimited pairs of ribs plus at least another two less obvious pairs. According to Bergeron the corresponding figures for the smaller holotype of *N. lignieresi* are eight rings and six pairs of ribs, but Thoral (1935*a* : 259) noted larger specimens of the species which differed from the holotype only in small details, and drew attention to one pygidium with seven axial rings and room for at least another three. The figured pygidium has parts of the surface ornamented with a pattern of raised ridges generally similar to that of the cranidium.

Although Bergeron's holotype was localized merely as " environs de St.-Chinian " he stated that the species occurred fairly frequently in the Montagne Noire, and later Thoral deduced that the specimen derived from the topmost Tremadoc Series of the district, at which horizon he had confirmed it. Additional, better-preserved material is needed before it can be confirmed that Bergeron's species is truly represented in the Couches du Landeyran inférieures. No specimens of *Niobella* have yet been found higher than this horizon in the Landeyran Valley–Le Foulon district.

A fragmentary cranidium from locality $\lambda 2$ is figured here as a latex cast (Pl. 15, fig. 3) and referred tentatively to *Niobella*. Its surface bears a conspicuous ornamentation of raised ridges similar to that on the cranidium illustrated (Pl. 15, fig. 2) as *Niobella* cf. *lignieresi*. The anterior border appears to be slightly thickened, but may have been exaggerated by crushing, whilst the anterior branches of the facial suture are strongly divergent at first, meeting frontally in a blunt point. The

facial suture compares with that of *Niobella fourneti* rather than *N. lignieresi*, but the pointed front of the cranidium is lacking in both these species and is more suggestive of the Tremadoc forms *N. obsoleta* Linnarsson sp. (see Tjernvik 1956 : 229) and *N. homfrayi smithi* Stubblefield (*in* Smith 1933 : 368).

Subfamily **OGYGIOCARIDINAE** Raymond 1937

Genus ***OGYGIOCARIS*** Angelin 1854

Ogygiocaris sp.

(Pl. 17, fig. 16)

FIGURED SPECIMEN. Brit. Mus. (Nat. Hist.) It.256.

LOCALITY AND HORIZON. λ32, about 240 metres south-west of Le Foulon, in the Couches du Landeyran inférieures.

DESCRIPTION. A single incomplete pygidium is the only specimen collected which may reasonably be assigned to this genus. Most of the right, and part of the left, side-lobe as well as the posterior half of the axis are preserved, and the estimated length and maximum breadth of the entire pygidium are 30 mm. and 47 mm. respectively. Although it is now slightly compressed the axis must originally have been narrow, its length four-fifths that of the pygidium. The posterior half of the axis is only gently convergent backwards, bounded by well-defined axial furrows and ends in a sub-rounded tip which stands well above the side-lobes. The hindmost 6 mm. or thereabouts of the axis are smooth, preceded by only a few traces of ring furrows. The frontal margin of the pygidium arches gently back to sub-rounded anterolateral angles behind which convex lateral margins converge to the broad tip which has a shallow (*sag.*), but nevertheless conspicuous, median indentation. The thin test has been replaced by limonitic material, some of which is exfoliated to reveal a broad doublure, its ventral surface carrying terrace-lines sub-parallel to the margin and its inner limit defined posteriorly by the tip of the axis. The right side-lobe carries seven unfurrowed pleural ribs, including apparently the anterior half-rib, of flattened appearance which extend abaxially back as far as the inner margin of the doublure, leaving a broad, almost flat border. Each rib is convex forwards in plan and subangular at about its centre, outside of which it turns backwards more strongly. In profile the ribs are asymmetrical, each with the anterior margin bevelled forwards to the steeper posterior margin of the preceding rib. The ribs are thus separated by broad (*exsag.*), shallow, pleural furrows which are fairly distinct until just beyond the margin of the doublure, where they then form barely discernible depressions which, in the case of at least the first two furrows, can be traced almost to the margin.

DISCUSSION. The type-species of *Ogygiocaris*, *O. dilatata* (Brünnich) from Stages 4aα and 4aβ of southern Norway, has been discussed and redescribed by Henningsmoen (1960 : 217). According to him the most characteristic feature of *Ogygiocaris* is the pygidium, and he sought to restrict the genus to species which possess a wavy

inner margin of the doublure and a similar paradoublural line on the dorsal test. Such an interpretation would mean excluding from *Ogygiocaris* all species hitherto referred to the genus which have been found outside Scandinavia, for example in Argentina and the Montagne Noire. More recently, however, Whittard (1964 : 231–245) has described and illustrated several species of *Ogygiocaris* from the Ordovician of the Shelve Inlier and has demonstrated that the features noted by Henningsmoen are not of generic significance. Accordingly it is preferred here to follow Jaanusson (*in* Moore 1959 : O 352) in regarding *Ogygiocaris* as a widely distributed Lower and Middle Ordovician genus found in Argentina, Europe and Scandinavia.

The single specimen from near Le Foulon is insufficient for a reliable comparison with other species of *Ogygiocaris*, but appears to have the pleural ribs turned backwards more sharply than do any of the forms illustrated by Henningsmoen (1960). It is easily distinguished from *Ogygiocaris? plana* and *O.? inflexicostata*, both from the Cabrières district (Thoral 1946 : 86, 89). The pygidium of the former species is broader and smoother, whilst that of the latter is broader with conspicuously strong, straight ribs, and I would agree with Henningsmoen (1960 : 214) that they should probably be excluded from *Ogygiocaris*. The pygidium of *O. araiorhachis* Harrington & Leanza (1957 : 157) is shorter and more rounded than the specimen now figured and has an entire, curved tip, whilst the pleural ribs, although about the same in number, are flatter and less curved backwards.

Of the species described and figured by Whittard (1964), *Ogygiocaris selwyni* (Salter) from the Lower Arenig has a pygidium which differs from our specimen in having a large concave border and more convergent lateral margins, whilst the tip, although blunt, lacks a median indentation. *O. seavilli* Whittard (1964 : 241), from the Lower Llanvirn Series, has a type of ribbing reminiscent of the Le Foulon pygidium but possesses several more ribs and a well-segmented axis.

Family **TAIHUNGSHANIIDAE** Sun 1931

Genus ***TAIHUNGSHANIA*** Sun 1931

1935*a*. *Miquelina* Thoral : 253.

Taihungshania landayranensis (Thoral)

(Pl. 16, figs. 1, 7)

1935*a*. *Miquelina miqueli* (Bergeron) var. *landayranensis* Thoral : 257, pl. 21, figs. 5–7.

Although described by Thoral as a variety of the better-known and more abundant *T. miqueli* (Bergeron), *T. landayranensis* seems sufficiently distinct for specific recognition and has been found only in the Schistes de Setso. The pygidium of *T. miqueli*, a typical specimen of which is figured here for comparison (see Pl. 16, figs. 3, 4), is longer and narrower than that of *T. landayranensis*, and the posterior margin is semi-elliptical as opposed to broadly rounded. In each case the pair of border spines is formed by extensions of the third pygidial pleurae, but those of *T. landayranensis* are notably longer, extending backwards beyond the tip of the pygidium.

The pygidial axis of *T. miqueli* is longer and narrower with more axial rings, and the side-lobes are well segmented carrying twelve to thirteen ribs in addition to the anterior half-rib, whilst those of *T. landayranensis* do not have more than seven or eight ribs.

A single specimen of *Taihungshania* from the Couches du Landeyran supérieures at locality $\lambda 19$ near the southern end of the Landeyran Valley, is the only record of the genus from the higher beds of the Ordovician succession in this district. It comprises a slightly compressed cranidium (Pl. 16, figs. 6, 8) which, as far as can be judged, differs from that of *T. miqueli* in having slightly smaller eyes placed closer to the glabella and a little farther forwards, as well as less divergent anterior branches of the facial suture. Sheng (1958 : 192–197) has described and illustrated from the Arenig and Llanvirn Series of south-west China a number of *Taihungshania* species, including *T. miqueli*, but none appears identical with the Landeyran Valley specimen.

Family **NILEIDAE** Angelin 1854

Genus ***SYMPHYSURUS*** Goldfuss 1843

Symphysurus sabulosus sp. nov.

(Pl. 18, figs. 4–7)

Diagnosis. Glabella subparallelsided posteriorly, expanding forwards so that basal breadth is two-thirds that of broadly rounded frontal glabellar lobe. Length and frontal breadth of glabella about equal. Occipital ring poorly defined, uniformly broad (*sag.*), curved forwards abaxially ; occipital furrow shallow, becoming obsolete near axial furrows. Anterior border and preglabellar field not developed. Eyes sited slightly in front of centre of glabella and only short distance from axial furrows.

Holotype. Brit. Mus. (Nat. Hist.) In.57729 (Pl. 18, figs. 4, 5, 7).

Paratype. In.57730 (Pl. 18, fig. 6).

Locality and horizon. Locality $\lambda 7$, about 480 metres south-west of Upper Bridge, in the northern part of the Landeyran Valley. The horizon is in flaggy calcareous sandstones, accompanied by slickensided shales, forming part of the Couches du Foulon.

Description. The species is known from only two incomplete, isolated cranidia preserved as internal moulds. The glabella is slightly more convex transversely than the adjacent parts of the cranidium, and becomes more strongly declined from back to front. In plan the sides of the glabella diverge forwards gently for half their length and then turn outwards more strongly to the rounded anterolateral angles, where they meet the broadly arched frontal margin. The projected length and frontal breadth are approximately equal, and about one and a half times the basal breadth. No glabellar furrows are discernible. The occipital ring is poorly differentiated, parallel-sided, curving forwards a little abaxially where the ends merge with the posterolateral portions of the glabella. The occipital furrow is represented by a shallow, curved groove, developed over only the median two-thirds of the basal

glabellar breadth. Though imperfectly known the pleuroccipital segment is narrow (*exsag.*), delimited by a sharply incised pleuroccipital furrow which is set behind the line of the occipital furrow (see Pl. 18, fig. 7). The axial furrows are broad, moderately deep, becoming shallower frontally, where they curve inwards slightly. There is no trace of a preglabellar field or anterior border, and the frontal margin of the glabella has the appearance of a sutural boundary. The palpebral lobes are unfurrowed, convex in plan, longitudinally just outside the line of the outer margins of the frontal glabellar lobe, and slightly in front of the glabellar centre. The anterior parts of the fixigenae are small and narrow, with the anterior branches of the facial suture slightly convergent forwards. The posterior parts of the fixigenae are set higher than the palpebral lobes and decline abaxially, particularly over their outer halves. The posterior branches of the facial suture curve outwards and strongly backwards from the eyes to the posterior cephalic margin, the basal projected breadth of each fixigena being about two-thirds that of the glabella.

Discussion. The type species of the genus, *Symphysurus palpebrosus* (Dalman) from the Middle Ordovician of Sweden, re-illustrated by Jaanusson (*in* Moore 1959, fig. 267–268), has a broader glabella, larger eyes and smaller fixigenae than *S. sabulosus*, and there is no trace of the occipital furrow. The well-known Scandinavian *S. angustatus* (Sars & Boeck), abundant in both the Tremadoc and early Arenig Series according to Tjernvik (1956 : 211), has a glabella which, although slightly narrower than that of *S. palpebrosus*, is broader than in the new species, though Brøgger's illustrations (1882, pl. 3, figs. 9, 10) suggest a certain amount of variation. The species most like *S. sabulosus* is that described by Brøgger (1882 : 58, pl. 1, figs. 1, 2) as *S. incipiens* from the Tremadoc Series of Norway. The latter has a glabella which, although broader basally than that of the French species, is nevertheless generally narrower and more expanded frontally than in other forms, whilst the posterior portions of the fixigenae of *S. incipiens* are almost comparable in size with those of *S. sabulosus*, but the eyes are larger.

Symphysurus has been found abundantly in the topmost Tremadoc Series of the Montagne Noire, where the species originally described by Bergeron (1895 : 478) as *Aeglina sicardi* was regarded by Thoral (1935*a* : 269) as a variety of *Symphysurus angustatus*. Bergeron's species, like most of the other forms of *Symphysurus*, has a broader, less expanded glabella and larger eyes than *S. sabulosus*.

Family **ODONTOPLEURIDAE** Burmeister 1843

Subfamily **SELENOPELTINAE** Hawle & Corda 1847

Genus ***SELENOPELTIS*** Hawle & Corda 1847

1847. *Polyeres* Rouault : 320 (see below).

It has recently been pointed out (Dean 1964) that *Polyeres* antedates *Selenopeltis* by several months, and that it can no longer be abandoned on the grounds of its being a junior subjective synonym of that genus, as has sometimes been alleged. Topotype material of the type-species, *Polyeres dufrenoyi* Rouault 1847, from the

Ordovician of Riadan, Brittany, leaves no doubt of the identity of the two genera. However, unlike the genus *Prionocheilus* Rouault 1847, discussed earlier in this paper, *Polyeres* was inadequately defined, no specimens have ever been illustrated, and the name has not been employed by systematists. For these reasons I propose here to reject *Polyeres* and retain the later, but well defined and illustrated, *Selenopeltis*.

In redefining both *Selenopeltis* and the Subfamily Selenopeltinae Whittington (1956 : 279 ; *in* Moore 1959 : O 508) stated that the occipital ring is short (*sag.*) with a single median tubercle. His description applies only to the type-species *Selenopeltis inermis* (Beyrich 1846) [=*Selenopeltis buchi* (Barrande 1846)], and in the present account it is preferred to modify this diagnosis of the genus so as to include the new species described below, in which there is a pair of small occipital spines, together with a small median tubercle, on a relatively long pseudoccipital ring composed of the normal occipital ring fused with the posterior part of the median body of the glabella. I prefer to follow Whittard's (1961 : 198) recognition of the priority of Beyrich's specific name, in spite of Vaněk's argument (1965 : 30) to the contrary.

Selenopeltis binodosus sp. nov.

(Pl. 20, figs. 4, 7, 8)

Diagnosis. Species of *Selenopeltis* in which posterior axial portion of cephalon is unusually long, consisting of occipital ring fused with transverse, convex band typically developed in this genus as a discrete structure traversing hindmost part of glabella. Third glabellar lobes large, divided into three parts by faint, transverse furrows, each posterior third so-formed being, in turn, divided into two by short, longitudinal furrow.

Holotype. Brit. Mus. (Nat. Hist.) It. 180.

Locality and horizon. Locality λ33 at the hillside section 250 metres south-west of Le Foulon. The horizon is in the Couches du Landeyran inférieures.

Description. The species is founded on a single incomplete, but distinctive, cranidium which is of depressed form and only slightly convex both longitudinally and transversely. The glabella is almost one and a half times as broad as long, nearly parallel-sided over its posterior half but narrowing a little frontally to just over half the basal breadth, with the anterolateral margins broadly rounded. There are three pairs of glabellar lobes, increasing markedly in size from first to third. The inner parts of the glabellar furrows do not end in-line, and the median band, the posterior half of which occupies two-fifths of the maximum glabellar breadth, narrows slightly from the second glabellar furrows. The third glabellar lobes are large, longitudinally subrectangular in plan, and of complex form. Each is divided into three parts, the first little more than half the size of each of the others, by two faint, transverse furrows. The first, or anterior part stands very slightly higher than the second, and appears to be defined by an abaxial bifurcation of the third

glabellar furrow, particularly at its inner end. In plan this part of the lobe narrows slightly towards the sagittal line and expands a little in the reverse direction, ending with a small lateral projection beyond the margin of the glabella. The median portion of the third glabellar lobe is flattened, subrectangular in plan, and its abaxial margin coincides with that of the rest of the glabella. The posterior portion, like the anterior one, is again slightly raised and its posterior margin is expanded backwards to form two small lobes. The inner lobe is slightly the larger and the two are separated by a shallow longitudinal furrow such as has been described from the corresponding part of the glabella of *Selenopeltis inermis* (Beyrich) by Whittington (1956 : 279 ; *in* Moore 1959 : O 508–509). The shallow furrows between the median and posterior thirds of the basal glabellar lobes are continued adaxially to form a deeper, broad (*sag.*) furrow traversing the median band of the glabella and gently concave forwards in plan. At first sight it would appear that the large structure immediately behind this furrow is nothing more than an extraordinarily large occipital ring. However, the furrow in question has its counterpart in *Selenopeltis inermis*, where it serves to delimit a basal portion of the median band of the glabella, and it appears that there is present what might be termed a pseudoccipital ring, composed of the normal occipital ring fused anteriorly with the posterior part of the glabella and bounded frontally by a pseudoccipital furrow. The maximum length of the pseudoccipital ring is equal to almost two-fifths of the distance between the pseudoccipital furrow and the front of the glabella. In plan it has curved lateral margins, extending forwards to the pseudoccipital furrow, and expands in breadth posteriorly. The dorsal surface is moderately inclined backwards, and the posterolateral margins are produced to form a pair of short, blunt, occipital spines, directed upwards and back. The anterior half of the pseudoccipital ring carries a trace of a low median tubercle. The second glabellar lobes expand a little in breadth (*exsag.*) towards the axial furrows and are separated from the median band by broad (*tr.*), shallow grooves. The outer halves of the third glabellar furrows are shallow and widely divergent forwards towards the axial furrows, but the adaxial portions are deep and arch backwards, ending opposite the mid-points of the third glabellar lobes. The second glabellar furrows are more gently curved back but uniformly deep, and widen (*exsag.*) a little adaxially. The first glabellar lobes are poorly defined, subrectangular in plan with their long axes widely divergent forwards, and bounded frontally by " perched " first glabellar furrows which do not reach the axial furrows. The axial furrows are shallow and poorly defined, whilst the fixigenae stand higher than the glabella at their apices, opposite the third glabellar lobes. They attain their maximum breadth here, about two-thirds that of the third glabellar lobes, but become narrower forwards, curve slightly inwards and end opposite the first glabellar lobes or the second glabellar furrows. Outside the fixigenae is a pair of slightly narrower ocular ridges, bounded adaxially by well-developed furrows which end anteriorly in-line with the small frontal glabellar lobe, from which they are separated by only the shallow frontal portions of the axial furrows. What remains of the anterior border forms a small, narrow (*sag.*) rim, its frontal margin transversely straight, truncated laterally by the incompletely-known anterior branches of the facial suture. Only traces of the

palpebral lobes remain, sited opposite the anterior two-thirds of the third glabellar lobes. The rest of the cranidium is not known.

A single incomplete thoracic pleura (see Pl. 21, fig. 6) was found at the type locality of *Selenopeltis binodosus* and shows the characters of the genus, as far as can be judged. The anterior pleural ridge is weakly developed but the anterior pleural spine is not preserved. The posterior pleural ridge curves gently forwards and outwards, and then more strongly backwards, being produced posterolaterally to form an elongated posterior pleural spine. Two conjoined thoracic segments of *Selenopeltis* from the Boutoury district are in an old collection at the University of Montpellier. They provide the only other evidence for the genus in the Montagne Noire, and may well belong to *S. binodosus*.

Discussion. Previously the earliest-known representative of *Selenopeltis* was *S. inermis macrophthalmus* (Klouček), described originally from the Šárka Beds (Llanvirn) of Bohemia (Klouček 1916 : 7 ; Prantl & Přibyl 1949 : 177) and since then found at a similar horizon in South Wales as well as in the Arenig and Llanvirn rocks of the Shelve Inlier (Whittard 1961 : 199). This trilobite differs from *Selenopeltis binodosus* in having a broader glabella and larger fixigenae which are less distinctly separated from the glabellar lobes, and almost coalesce with the anterior halves of the second lobes. More striking differences are found in the posterior third of the glabella and the occipital ring, a region of the exoskeleton which has been described by Whittington (1956 : 279 ; *in* Moore 1959 : O 508) who showed that in the type species *Selenopeltis inermis* (Beyrich) [=*S. buchi* (Barrande)] the hindmost portion of the median lobe of the glabella was traversed by a shallow furrow. His illustrations show the outer ends of this furrow to be sited opposite a pair of transverse furrows crossing the third glabellar lobes, and it is only behind these furrows that the third lobes are subdivided by a pair of shallow, longitudinal furrows. The transverse furrow on the median glabellar lobe is not apparent in the illustrations of Prantl & Přibyl (1949 : 175), nor in those of Barrande (1852, pl. 36, figs. 1, 8, 9 ; pl. 37, fig. 25). By analogy with Whittington's description the front of the apparent occipital ring (here pseudoccipital ring) of *Selenopeltis binodosus* must therefore correspond to the transverse furrow in front of the occipital furrow of *S. inermis*, so that a normal occipital furrow is not developed in the French species. Alternatively one could interpret the anterior of the two pairs of transverse furrows crossing the third glabellar lobes of *S. binodosus* as marking the position of the furrow, here obsolete, traversing the glabella. Against this argument, it must be pointed out that the median thirds of the third glabellar lobes carry no traces of longitudinal furrows. The position would probably be clarified if further material were available, but the present interpretation at least attempts an explanation of the extraordinarily long occipital ring of *S. binodosus*.

It is interesting that both Prantl & Přibyl (1949 : 173) and Whittington (1956 : 280) have commented on the affinities of *Selenopeltis* with the Subfamily Miraspidinae. The genus *Miraspis* has paired spines at the ends of the occipital ring, together with a median tubercle on the posterior part of the median band of the glabella. All these

structures have their counterparts in *Selenopeltis binodosus*, but paired occipital spines are unknown in *S. inermis*.

The Breton species *Polyeres dufrenoyi* Rouault 1847 is in need of redescription but is obviously related to *Selenopeltis inermis*, as was appreciated by Barrande. A topotype in the British Museum (Natural History), no. I.15373, is distorted but the pygidium, with its relatively coarse ornamentation, resembles that of *Selenopeltis inermis inermis* rather than *S. inermis macrophthalmus*.

Family **OTARIONIDAE** R. & E. Richter 1926

Genus ***OTARION*** Zenker 1833

Otarion insolitum sp. nov.

(Pl. 19, figs. 11, 13, 14)

Diagnosis. Glabella subtrapezoidal in plan, broader than long, with pair basal glabellar lobes. Deep, broad, continuous furrow circumscribes glabella and straight sides converge forwards to almost straight anterior margin. Eyes positioned just behind line through centre of glabella. Preglabellar field well developed, with length more than one-third that of glabella, bounded frontally by low, narrow (*sag.*) anterior border.

Holotype. Brit. Mus. (Nat. Hist.) In.57452.

Locality and horizon. Locality λ19 near the southern end of the Landeyran Valley. The horizon is in the Couches du Landeyran supérieures.

Description. The species is known from only a single small cranidium, a little less than twice as broad as long. Its convexity is only moderate, both longitudinally and transversely, but both this and the proportions may have been altered a little by compression. The length of the glabella is about three-quarters of its basal breadth, whilst the glabellar outline is roughly trapezoidal, with its frontal margin only very slightly convex forwards. There is one pair of basal glabellar lobes, subcircular in plan, about one-third the glabellar length, circumscribed, and separated from the remainder of the glabella, by deep, broad furrows. The sides of the glabella are almost straight, particularly in front of the basal lobes, and converge forwards at about 40° to the rounded anterolateral angles of the frontal glabellar lobe. The frontal breadth of the glabella is half the basal breadth. The axial furrows are straight, deep, and apparently uniformly broad. The slight indentation of the right axial furrow by the basal glabellar lobe is probably mechanical in origin. The axial furrows turn through almost 70° at the anterolateral angles of the glabella and are confluent with the equally broad (*sag.*) preglabellar furrow. The preglabellar field is well developed, its length (*sag.*) equal to between one-third and one-half that of the glabella. It is moderately declined forwards where it meets the narrow (*sag.*), upturned, rim-like anterior border at a poorly-defined anterior border furrow. The occipital ring is short (about one-fifth the glabellar length), convex, separated from the glabella by a transversely straight occipital furrow which is indented by the basal

glabellar lobes. The pleuroccipital furrow is mostly transversely straight, curving back a little distally. The pleuroccipital segment is narrow (*exsag.*) just outside the axial furrows and becomes slightly wider distally. The palpebral lobes are smooth, rounded in plan, sited opposite a point just behind centre of the glabella. The anterior branches of the facial suture follow a sigmoidal course, converging forwards at first until almost opposite the preglabellar furrow; they then diverge as far as the anterior border furrow, when they again converge, this time more sharply so as to intersect the cephalic margin at an acute angle. The posterior branches are less well preserved but appear to be typical for the genus, that is to say they are almost straight, running backwards and outwards to cut the posterior cephalic margin. The surface of the holotype shows no ornamentation, probably owing to its preservation as an internal mould. The remainder of the exoskeleton is unknown.

DISCUSSION. *Otarion insolitum* is probably the oldest-known representative of the genus, and may be distinguished from younger Ordovician species by its more angular, convergent glabellar outline and longer preglabellar field. Cooper (1930 : 377–378), when describing *Otarion* [*Cyphaspis*] *minimum* from the Upper Ordovician of Quebec, drew attention to the " extremely long frontal border " of that species, presumably referring to the combined preglabellar field and broad (*sag.*) anterior border. The preglabellar field of *O. insolitum* is still longer (*sag.*) than that of *O. minimum* whilst the anterior border is much narrower, but the combined length of these structures is greater than that of the Canadian species. Previously *Otarion* was unknown from pre-Middle Ordovician rocks, and *O. insolitum* is of particular interest in illustrating the small changes undergone by the cephalon of the genus during a remarkably long span of time.

Family **PROETIDAE** Salter, 1864

Proetid gen. et sp. indet.

(Pl. 15, figs. 1, 7)

FIGURED SPECIMEN. A cranidium, the only known specimen, in the collections of the University of Montpellier.

LOCALITY AND HORIZON. The specimen is labelled merely as " Le Foulon " and probably comes from the outcrops south-west of that building (see Text-fig. 5). The horizon is almost certainly the Couches du Landeyran inférieures.

DESCRIPTION. The cranidium is apparently only slightly convex, though this has probably been exaggerated by crushing, judging from the fractures of the test. The occipital furrow is barely discernible, so that the glabella and occipital ring are almost continuous. There are no glabellar furrows and the combined glabella and occipital ring are subtriangular in plan, bounded by straight, shallow, axial furrows which converge forwards at about 35° and are continuous with a preglabellar furrow of similar depth which circumscribes the narrowly rounded, frontal glabellar lobe.

The anterior border is flattened, brim-like, becoming a little narrower (*sag.*) abaxially but with a median breadth equal to one-seventh of the length of the cranidium. The anterior border and glabella are separated by a gently declined preglabellar field which is narrowest medially, where its breadth equals that of the anterior border, but broader abaxially to merge with the large frontal halves of the fixigenae. The palpebral lobes are only slightly convex and situated relatively far from the glabella ; they converge forwards, parallel to the axial furrows, and carry faint palpebral furrows. The length of the palpebral lobes is one-fifth that of the cranidium, and their anterior ends are situated a little in front of a line through the centre of the glabella. The anterior branches of the facial suture diverge at approximately 40° and are straight as far as the anterior border, where they curve inwards through about 60°, run at an acute angle to the cephalic margin and meet frontally in a broad arc. The posterior branches curve outwards and back so as to cut the posterior margin well outside the line of the palpebral lobes. The pleuroccipital furrow is about level with or slightly behind the conjectured position of the occipital furrow, whilst the posterior margin of the pleuroccipital segment is set slightly in front of that of the occipital ring. Markedly narrow (*exsag.*) immediately outside the axial furrows, the pleuroccipital segment broadens a little abaxially. As far as can be judged, the whole of the cranidial test is smooth.

DISCUSSION. The history of the proetid trilobites during the Ordovician is poorly documented, and undoubted representatives have not been described prior to the Middle Ordovician. No comparable species have been illustrated, and additional material would probably require the erection of a new genus. An unusual feature is the manner in which the glabella and occipital ring are united, but the anterior border, preglabellar field and form of the facial suture resemble those of the proetids, whilst the triangular glabellar outline is not uncommon, as for example in *Clypoproetus* Begg, from the Upper Ordovician, and numerous other, later genera.

Family **REMOPLEURIDIDAE** Hawle & Corda 1847

Subfamily **RICHARDSONELLINAE** Raymond 1924

Genus ***APATOKEPHALUS*** Brögger 1896

Apatokephalus incisus sp. nov.

(Pl. 20, figs. 1–3, 5, 6, 9 ; Pl. 21, figs. 1–4, 7)

DIAGNOSIS. *Apatokephalus* with three pairs straight glabellar furrows, all sited behind large, broad glabellar tongue. First and second pairs meet palpebral furrows ; third pair developed only adaxially and does not traverse glabella. Preglabellar field narrow (*sag.*). Anterior border furrow contains series of pits. Long, curved, librigenal spines developed well forwards, opposite mid-points of palpebral lobes and outside pair of large notches in posterior margin of librigenae. Pygidium with small triangular axis and three axial rings. Pleural lobes end in three well-defined

pairs of pleural spines, with diminutive fourth pair. First and second pairs spines end in-line, remaining spines stepped forwards successively.

HOLOTYPE. Brit. Mus. (Nat. Hist.) It.176 (Pl. 20, figs. 1, 2).

PARATYPES. In.57422 (Pl. 21, figs. 3, 7); It.177 (Pl. 20, fig. 3); It.179 (Pl. 20, fig. 6); It.182 (Pl. 21, fig. 2); It.183 (Pl. 20, fig. 9; Pl. 21, fig. 4); It.287 (Pl. 20, fig. 5).

LOCALITIES AND HORIZON. The species was found most commonly at the hillside section 250 metres south-west of Le Foulon, where it was collected from localities $\lambda 30$, $\lambda 31$ and $\lambda 33$, particularly the last. In the Landeyran Valley *Apatokephalus incisus* has been found at two localities, both near the northern end of the valley. The better-preserved and more abundant material is from locality $\lambda 2$, but a slightly distorted cranidium with attached thorax was found at locality $\lambda 4$. In the present area all the known specimens are from the Couches du Landeyran inférieures, and the species occurs also in the Boutoury district, probably at the same level.

DESCRIPTION. The cephalic outline is rounded, sub-semicircular frontally, the length, including librigenal spines, being almost one-and-a-sixth times the maximum breadth as measured across the spines, well behind the line of the occipital ring. The glabella is known only from specimens which have been slightly compressed so that accurate proportions are difficult to determine, but the median projected length is probably about five-sixths of the maximum breadth. The posterior portion of the glabella, occupying approximately two-thirds of the projected length, is transversely subellipitical in outline, but the anterior portion extends forwards to form a glabellar tongue, the basal breadth of which is almost half the maximum breadth of the glabella. Three pairs of unequal glabellar lobes are present. The first pair are the smallest, rectangular in plan and bounded frontally by short (*tr.*) first glabellar furrows which resemble straight, narrow incisions and run inwards and backwards at an angle of 50° to the sagittal line. At their outer ends the first glabellar furrows intersect the forward extension of the palpebral furrows and indicate the base of the glabellar tongue. The second glabellar furrows are narrow, straight, parallel to the first pair but more than twice as long (*tr.*), and extend inwards a little farther; they, too, cut the palpebral furrows. The third glabellar furrows do not extend so far abaxially as the second furrows and are only about half their length. Consequently the second and third glabellar lobes are developed separately for only about one-third their length and fuse together abaxially, the third lobes being slightly the wider (*exsag.*), with their anterolateral margins slightly expanded. The large dimensions of the glabellar tongue have already been noted. Here it corresponds also to the frontal glabellar lobe, though this is not always so in remopleuridids, as the glabellar tongue may include also the first glabellar lobes. In specimens which have been dorsally compressed the glabellar tongue sometimes appears longer than was actually the case, and the manner in which it was turned down frontally is not now obvious. The tongue expands forwards only slightly and its anterior margin is moderately convex, bounded by a shallow preglabellar furrow. Immediately in front the preglabellar field is narrow (*sag.*) medially but broadens abaxially; it is separated from the

anterior border by a broad, shallow, anterior border furrow which can sometimes be seen to contain a number of pits, such as are known from other genera of the Richardsonellinae. The maximum number of pits found preserved in any one specimen is eight or nine, but the original number must have been greater, probably nearer fifteen in the largest cephala. The anterior border has a frontal breadth (*sag.*) rather more than twice that of the preglabellar field, and is continuous posterolaterally with the lateral borders. The dorsal surface of the anterior border is nearly flat and must originally have been in the same plane as the posterior portion of the glabella, that is to say almost at right-angles to the strongly declined glabellar tongue, though this relationship is generally obscured by crushing in an argillaceous matrix. The librigenae are narrow with raised, ridge-like, lateral borders marked off by broad lateral border furrows forming continuations of the anterior border furrow. Their lateral margins are curved and they are produced backwards to form a pair of long librigenal spines which arise from points level with the mid-points of the palpebral lobes and arch outwards slightly until behind the line of the occipital ring, when they become gently convergent, ending in slender points. The inner margins of the librigenal spines are separated from the hindmost parts of the librigenae by large, triangular notches, the adaxial margins of which are straight, converging backwards to meet the posterior cephalic margin outside the lines of the palpebral lobes. The visual surfaces of the eyes have not been found, but their lower boundaries were circumscribed by narrow eye platforms. The occipital ring is trapezoidal in plan, transversely parallelsided with the straight lateral margins running backwards and slightly outwards and bounded by deep axial furrows, and is separated from the glabella by a uniformly deep occipital furrow. The palpebral lobes are large, elongated, semi-elliptical in outline with flattened dorsal surface. They are uniformly narrow for most of their length but the hindmost portions become broader opposite the inner ends of the third glabellar furrows, at the same time flexing more sharply inwards and ending with their posterior margins opposite the occipital furrow. The frontal part of each palpebral lobe continues forwards as a narrow rim, running below and alongside the glabellar tongue and merging frontally with the fixigena. The palpebral furrows are moderately deep and broad along the anterior two-thirds of the palpebral lobes but become deeper and narrower posteriorly, where they follow a sinuous course and converge backwards to join the outer ends of the occipital furrow. Frontally they become narrower and shallower, and run into the furrows flanking the glabellar tongue, which in turn coalesce with the preglabellar furrow. From each axial furrow the pleuroccipital segment extends outwards for only a short distance, approximately equal to two-thirds of the breadth (*tr.*) of the occipital ring. It widens (*exsag.*) abaxially for about two-thirds of its length (*tr.*), then narrows more sharply to a blunt point, and carries a broad (*exsag.*) pleuroccipital furrow which is transversely straight in direction and set in-line with the hindmost part of the occipital ring. The anterior branches of the facial suture are long and follow a markedly flexuous path; they at first curve forwards only a little way from the front ends of the eyes, then turn outwards and back, and run subparallel to the lateral border furrows until slightly beyond the line of the palpebral lobes, where they flex

forwards sharply through almost 180°, cutting the anterior border obliquely and finally converging frontally below it.

The thorax has not been found completely preserved but comprises at least nine segments of generalized remopleuridid aspect. The axis is moderately convex, fairly broad (about half the thoracic breadth), and is delimited by deep, narrow axial furrows. The axial rings are rectangular in plan, the breadth (*sag.*) between one-quarter and one-fifth of the length (*tr.*). The pleurae are broadly similar to those of *Remopleurides*, that is to say flattened, parallel-sided, directed outwards and slightly backwards from the axial furrows for about half their length and then narrowing sharply to form short, curved pleural spines directed posterolaterally. Broad (*exsag.*) pleural furrows run backwards abaxially from the anterior margins of the pleurae at the axial furrows. The pleural furrows are deep and straight at first but then become fainter and curve backwards, though without reaching the tips of the pleural spines.

The pygidium is of depressed form, slightly more than one-and-a-half times as broad as long, its outline well rounded frontally, except at the axis, and ending in a spinose posterior margin. The axis is small, triangular in plan, with frontal breadth about one-third the maximum breadth of the pygidium. It has straight sides converging backwards at about 55° and marked by narrow, moderately-deep axial furrows which become slightly shallower and less well defined as they meet at the pointed axial tip. There are three axial rings, followed by a triangular terminal piece occupying about, or slightly more than, half the length of the axis. Immediately behind the third axial ring of one specimen (Pl. 21, fig. 4) is a small median node, about one-third the frontal breadth of the terminal piece and almost half its length. This is apparently an original feature but as the corresponding portion of the only other available pygidium is damaged, there is no certainty that it is not the result of crushing. The side lobes are large, wide and flattened, composed of four pairs of pleurae which decline in size from first to fourth, at the same time becoming more strongly arched backwards until the fourth pair are parallel to each other. The first two pleurae end in large, curved, free spines, the length of each being about one third that of the pleura, and the pointed tips end in-line with one another posteriorly. The spines formed by the third pleurae are notably smaller, their tips stepped forwards, whilst the fourth pair of spines is represented by a pair of tiny projections arising from pleurae which are small and scarcely discernible. Each of the first three pleurae is divided into two bands by a deep, broad (*exsag.*), pleural furrow which becomes less distinct towards the tip of the pleural spine. The anterior band is only about half the size of the posterior band.

The hypostoma has not yet been found and the underside of the exoskeleton is poorly known, but the ventral surface of the librigenal spines carries a series of thin, longitudinal, raised ridges. The doublure is well developed on both thorax and pygidium, in the latter case extending inwards almost level with the tip of the axis. The ventral surface of the doublure is ornamented with closely grouped terrace-lines.

The surface of the glabella is covered with closely-grouped, coarse granules, except at and near the glabellar furrows (see Pl. 21, fig. 3). Similar ornamentation is found

on the occipital ring and the axial rings of the thorax, but has not yet been traced on the anterior border, palpebral lobes, thoracic pleurae or pygidium, the test of which is either smooth or very finely granulated.

DISCUSSION. The type-species of *Apatokephalus*, *A. serratus* (Boeck), was described originally from the Ceratopyge Limestone (Tremadoc Series) of the Oslo region, and has been redescribed and illustrated from Scandinavia by a number of authors, particularly Brøgger (1882 : 126, pl. 3, figs. 7, 8), Moberg & Segerberg (1906 : 88, pl. 5, figs. 9, 11) and, more recently, Tjernvik (1956 : 204, pl. 2, figs. 7, 8, text-fig. 32A). A line restoration of the species published by Whittington (*in* Moore 1959 : O 329, fig. 243–2a, b) differs in several respects from that provided by Tjernvik. The latter author's illustration of the librigena shows the genal spine arising from a point well forward of the line of the pleuroccipital furrow, resulting in the formation of a large notch adjacent to the genal spine. Conversely the librigena figured by Whittington shows only a trace of such a notch and the genal spine runs backwards almost from the genal angle. The third glabellar furrows of Whittington's illustration are shown as gently sigmoidal grooves developed only adaxially, with the straight second furrows almost reaching the axial furrows, whilst the first furrows are straight, directed outwards and slightly backwards, ending slightly farther from the axial furrows than do the second furrows. In Tjernvik's restoration the third glabellar furrows are more strongly divergent forwards and extend a little nearer the axial furrows, whilst both the second and first glabellar furrows are straight, running backwards and inwards from the axial furrows. The apparently shorter glabellar tongue of Whittington's illustration could well be accounted for by differences in preservation and relative position of the cephalon. The form of the pygidium is generally similar in both sets of drawings, but whilst Whittington's diagnosis of the genus claims there are only five pairs of pleural spines, according to Tjernvik there are six or seven pairs, numbers which are supported by Brøgger's illustrations of the species (1882, pl. 3, figs. 7, 8). The pygidium of *Apatokephalus incisus* has only four pairs of pleural spines, an unusually small number for the genus, but the importance of this feature should not be overestimated in view of the fact that specimens of *A. serratus* with from five to seven pairs of spines have been illustrated.

"*Apatokephalus serratus* (Sars & Boeck) " as described and illustrated from the Marathon Uplift of Texas by Wilson (1954 : 275, pl. 27, figs. 1, 2, 13) appears to be distinct from the Scandinavian form and to represent a new species, for which the name *Apatokephalus wilsoni* nom. nov. is now proposed. It is particularly characterized by its conspicuously convex, broad, glabellar tongue, notably larger than in other species of the genus, with the palpebral lobes projecting only a relatively short distance beyond the line of its lateral margins. In addition, the anterior border is unusually convex forwards in plan, separated from the well-rounded frontal glabellar lobe by only a narrow (*sag.*) furrow containing a number of pits.

The new species bears a considerable resemblance to *Menoparia*, described from the Garden City Formation of Utah by Ross. The type-species, *Menoparia genalunata* Ross (1951 : 88, pl. 20, figs. 13–24, 28, 29, 34–5), has a pygidium in which the develop-

ment of pleural lobes and spines is much the same as those of *Apatokephalus incisus* but the axis is much larger and longer. The cephalon of the American form has a facial suture and anterior border like those of *A. incisus*, but the latter species lacks the axial furrows of *M. genalunata*, probably a much more significant feature for generic distinction than the pygidium. For the same reason it is unlikely that *Menoparia? nericiensis* Tjernvik (1956 : 206, pl. 2, fig. 9–11, text-fig. 32B), from the Arenig Series of Sweden, truly represents that genus, and in some respects the species more resembles a genuine *Apatokephalus*. The pygidium of *M.? nericiensis* is broadly similar to that of *Apatokephalus incisus*, differing in having a small postaxial ridge, and third pleural spines which are slightly longer than the first and second pairs. The librigena of the Swedish species has almost no development of a genal notch and the cranidium carries only two pairs of glabellar furrows, but the cephala are otherwise alike in all essential features. The pygidium of *Eorobergia marginalis* (Raymond), the type-species of *Eorobergia* Cooper (1953 : 21, pl. 8, figs. 1–6), from the Middle Ordovician of Tennessee, differs from that of *Apatokephalus incisus* in having the third and fourth pleural spines longer than the first and second pairs, and also, like *Menoparia*, in possessing a conspicuously larger axis. The cephalon of *Eorobergia* is like that of *A. incisus*, particularly in the plan of the palpebral lobes and the disposition of the glabellar furrows, though the first and second pairs are less well defined, but the anterior branches of the facial suture flex outwards only a little way, and consequently the cranidium does not have the large, lateral projections of the anterior border which are so conspicuous a feature of the cranidium in the French species.

One other remopleuridid trilobite has been described from the Arenig Series of the Montagne Noire, namely *Apatocephalus* [*sic*] *brevifrons* Thoral (1935*a* : 293, pl. 19, figs. 5, 6). The species was founded on three syntypes, all cranidia, two of them from a siliceous nodule collected " 400 metres west of Prades-sur-Vernazobre " (a village between Lugné and St. Chinian), the third from an undefined locality near St. Chinian. The original of Thoral's pl. 19, fig. 5, a specimen in the collections of the University of Montpellier, is chosen here as lectotype and a cast of it is refigured (see Pl. 21, fig. 5). Although the glabellar furrows of *A. brevifrons* are in positions generally similar to those of other species of the genus, they are much longer (*tr.*) leaving only a narrow median band, and even this appears to be traversed by a groove connecting the third glabellar furrows. In addition all the glabellar furrows are uniformly and markedly deep, and intersect the palpebral furrows. The glabellar lobes so formed have well-rounded tips which bulge beyond the outer ends of the glabellar furrows, the second lobes being conspicuously clavate in outline. The dorsal surface of the glabella is less flattened than in other species of *Apatokephalus*, the glabellar tongue is unusually small and convergent forwards, and it is likely that additional material of this species would necessitate the erection of a new generic name.

A Norwegian cranidium purporting to be that of *Apatokephalus serratus* was figured by Størmer (1922, pl. 2, fig. 3). The third glabellar furrows of this specimen are apparently confluent across the median band of the glabella and Tjernvik (1956 :

205) has suggested that it probably represents a new species. As described above, such a continuation of the third glabellar furrows may be an original character in *Apatokephalus? brevifrons* Thoral, but similar features have been found in *Apatokephalus incisus* and in this case there can be little doubt that the supposed median portion of the furrow is the result of crushing.

V. RELATIONSHIPS OF THE SHELLY FAUNAS

Some years ago Stubblefield (1939), in discussing the Lower Palaeozoic trilobite faunas of the British Isles, noted that it was possible to delimit certain faunal provinces there. He showed that the Lower and Middle Ordovician faunas of what he called the " Scots–Irish Area " closely resembled those of eastern North America, whilst contemporaneous faunas of the Anglo–Welsh area showed affinities with Bohemia and southern Europe. His observations matched those published later by Spencer (1950) on the corresponding echinoderm (Asterozoan) faunas. Since then Spjeldnaes (1957) has discussed the distribution of Ordovician climatic zones with particular reference to Europe and Scandinavia, equating them in the process with faunal provinces, in a paper which, in some respects, tends to oversimplify the problems by grouping together various deposits of different ages. His map of the " Middle Arenig " province shows the Montagne Noire as one with the south-eastern half of the Iberian Peninsula, forming a " trilobite facies, mudrock in Mediterranean province ", merging to the south with the south-eastern extremity of the " Armorican Quartzite " of western France, the north-western Iberian Peninsula, and extending into North Africa. This region is separated by him from Bohemia. According to Spjeldnaes the Mediterranean Province extended eastwards to Syria, but this appears to be an underestimate and the Arenig faunas suggest an extension at least as far as south-western China.

In a recent review of Ordovician faunal provinces Whittington (1963 : 18–23) noted three as existing during Upper Arenig times, namely a Bathyurid province (covering North America, Greenland, and the Caledonian belt of western Norway, north-west Scotland and western Ireland), an Asaphid province (southern Scandinavia and the Baltic region), and a Calymenid-trinucleid province (comprising Wales, central England, and a belt extending longitudinally south-westwards from Central Europe to Morocco by way of France and the Iberian Peninsula). It is with the last-named province that the faunas of the Montagne Noire, and others in the Mediterranean region, are primarily concerned. Whittington (1963 : 20) believed this province to have been less well defined during Arenig times than in the Llanvirn–Llandeilo, but the present evidence suggests that the general pattern was established at least as early as the lower Arenig. As Whittington noted, the genera *Geragnostus* and *Ampyx* are common to all three provinces, and the former was already widely distributed in Upper Cambrian and Tremadoc faunas.

The faunas described in the present paper refer only to the eastern end of the principal Ordovician outcrops on the southern flanks of the Montagne Noire. To the west the successions around Prades-sur-Vernazobres, St. Chinian, and south of

Coulouma have still to be examined in detail, but there are certainly marked facies changes in that direction, and the sandstones of the Grès à Lingules and Couches du Foulon die out. Similarly the black, graptolitic Schistes de Setso, containing *Taihungshania landayranensis*, may be represented near St. Chinian by mudstones and shales in Thoral's zone of *Taihungshania* [*Miquelina*] *miqueli*, the only other horizon at which the characteristic trilobite genus is at all common in this region. The exact line of demarcation between the Tremadoc and Arenig Series in the St. Chinian district (*s.l.*) is not so sharply defined as might appear from the published accounts, but the strata of late Tremadoc–early Arenig age have yielded, over the years, numbers of siliceous nodules containing trilobites, molluscs and carpoids. This facies, and the included fauna, is closely paralleled by that of the younger Šárka Beds (Llanvirn Series) in the Rokycany district of Bohemia, as well as by the strata of Le Traveusot in Brittany, suggesting a northward extension of the province from Arenig to Llanvirn times. East-north-east of the Landeyran Valley the faunas of all the Couches du Landeyran are well represented in collections from the Boutoury district, just north of Cabrières, whilst the trilobites of the one-time " Schistes à Gateaux " at Cabrières, described by Thoral (1946), suggest at least a partial correlation with the Couches du Landeyran inférieures. The map of this region published by Chazan (1939) did not subdivide the Arenig succession, and there is no indication that the lateral equivalents of the Grès à Lingules are present, but some of the type material of *Taihungshania miqueli*, the index-fossil of the basal Arenig near St. Chinian, was described by Bergeron (1893 : 334) from Boutoury.

The Ordovician stratigraphy and faunas of the Méséta marocaine occidentale (the region south-west of Casablanca) were described by Gigout (1951) who noted their Franco–Bohemian affinities. In a later paper (1956) he revised the stratigraphical position of the strata and divided them as follows : basal quartzites ; two successive shaly series with graptolites suggesting the lower and upper zones of the Arenig Series ; and a shaly, sandy series containing numerous trilobites and the Lower Llanvirn index-fossil *Didymograptus bifidus*. The highest series was followed unconformably by Silurian strata, a state of affairs broadly paralleled in the Montagne Noire, where Arenig strata are followed as a rule by Devonian beds or, in certain areas such as that of Neffiès, some 20 km east-north-east of the Landeyran Valley, by a thin, fragmentary Ordovician succession of alleged Caradoc and Ashgill strata and then an incomplete Silurian sequence. Although the Moroccan species *Neseuretus attenuatus* (Gigout) has not yet been confirmed in the Montagne Noire, as was claimed by Gigout, nevertheless there can be no doubt that certain genera are common to both regions, and the resemblance of Gigout's " *Calymene* aff. *pulchra* " to *Bathycheilus gallicus* was noted earlier. Further evidence of these faunal affinities is provided by Gigout's discovery (1954) in Morocco of the carpoid *Phyllocystis blayaci* Thoral, a species first described from the upper Tremadoc and basal Arenig Series near St. Chinian (Thoral 1935*a* : 104). Gigout has used the fact that the Moroccan specimens are supposed to occur at a slightly later horizon to support his suggestion that *Phyllocystis*, together with certain trilobites from the Montagne Noire, migrated towards Morocco from the north. In fact, the records of species common to both

regions appear to be of at least broadly comparable age, namely Lower Arenig (=Extensus Zone). Other Montagne Noire species, or forms close to them, recorded from Morocco are *Niobe fourneti* Thoral and *Plesiomegalaspis graffi* Thoral (see Gigout 1951 : 282–283 ; Van Leckwijck *et al.* 1955 : 15). These two species occur in the Cabrières faunas and, if truly present in North Africa, suggest a large lateral distribution of the appropriate strata or their probable equivalents, the Couches du Landeyran inférieures. More recently Destombes (1963 : 152) has recorded from the Lower Arenig of the Anti-Atlas several trilobite families which occur at the same horizon in the Montagne Noire.

Judging from the published lists of Ordovician trilobites from Bohemia (see, for example, Havlíček *et al.* 1958) there was little connection between that region and Hérault during early Arenig times, the genera common to both including only *Geragnostus* and *Pliomerops* (see earlier). However, one of the most striking features of the Arenig faunas in the Montagne Noire is the large number of genera which probably migrated from there to Bohemia, and are not known from that region prior to the Llanvirn Series. A notable example is the dalmanitid *Ormathops*, previously unrecorded from the Arenig Series but widespread in European Llanvirn strata. *Ormathops borni* (see earlier) of the Landeyran Valley outcrops almost certainly includes the forms listed by both Born (1921) and Thoral (1933 : 148) as *Dalmanites socialis* Barrande, the type-species of *Dalmanitina*. The latter genus is characteristically later in age, and in the Montagne Noire has been recorded, as *Dalmania socialis* var. *grandis* (Barrande) and var. *proaeva* (Emmrich), only from the supposed Caradoc strata of the Grand Glauzy, in the Neffiès district, where it occurs in company with *Cryptolithus grenieri* (Bergeron) and *Kloucekia* [*Dalmania*] *exophtalma* (Dreyfuss 1948), an assemblage having affinities with north-western France. The Arenig *Bathycheilus gallicus* of the Landeyran Valley was followed by *B. perplexus* in the Bohemian Llanvirn, whilst a similar distribution holds good for the more widespread calymenaceids *Colpocoryphe* and *Prionocheilus* as well as the rare nileid *Kodymaspis* (see Prantl & Přibyl 1949*a* : 6), represented in the Arenig by *Platypeltis*? *macrophthalmus* Thoral (1935*a* : 273) and in the Llanvirn by *Illaenus puer* Barrande (1872 : 73).

In north-western France, according to Dangeard (1951 : 42, 46) the Lower Ordovician is represented by the almost unfossiliferous Grès armoricain, and, as in Bohemia, it is not until later that the full effects of the migrations from the Mediterranean region are fully seen. The true " Schistes à Calymènes ", the type development of the so-called " *tristani* fauna ", belong mainly to the *Didymograptus murchisoni* Zone (Phillipot 1950), and although *Neseuretus*, *Colpocoryphe*, *Prionocheilus* and *Selenopeltis* are known from the Arenig of Hérault, they are joined here by *Placoparia*, *Dalmanitina* and asaphids, all of definite Bohemian type and as yet unknown below the Llanvirn. A similar state of affairs exists at about this horizon in Portugal (see Delgado 1908 ; Curtis 1961), where we also find the Bohemian *Bathycheilus perplexus* (Thadeu 1958), as well as in Spain, where the *Neseuretus tristani* fauna is well developed (Born 1918).

The Llanvirn trilobite faunas of the Anglo-Welsh area have remarkably close

affinities with those of Bohemia, whilst those of the Arenig Series have several genera in common with the Montagne Noire, for example *Geragnostus*, *Ampyx*, *Neseuretus*, *Selenopeltis* and *Ogygiocaris*. The trinucleid *Myttonia*, though not known outside the area, nevertheless has affinities with *Hanchungolithus* and is placed in the same subfamily. The absence of *Colpocoryphe* is a curious feature of the Anglo–Welsh faunas, but the rare *Platycoryphe* of the Landeyran Arenig is followed by a greater abundance of the genus in the Llanvirn of the Shelve Inlier. The trilobites of both the Arenig and Llanvirn Series in the Anglo–Welsh area occur mostly in argillaceous sediments, and consequently are generally accompanied by large numbers of molluscs, particularly bivalves and gastropods, and phyllopods. They share this character with the corresponding faunas of Bohemia, north-western France, the Iberian Peninsula, the Montagne Noire and North Africa, and certain genera persisted through a long span of geological time with relatively little modification. *Redonia*, described first by Rouault (1851 : 362) from Brittany, is a particularly conspicuous member of the bivalve fauna, whilst the supposed phyllopod *Ribeiria*, founded by Sharpe (*in* Ribeiro 1853 : 157) on Portuguese material, occurs in the Montagne Noire (Thoral 1935*a* : 171) as well as the Shelve Inlier, where it is represented by *R. complanata* (Salter *in* Salter & Etheridge 1881 : 551).

Whittington's record (1953) of *Colpocoryphe* in Florida suggests a possible western limit for the Mediterranean Province, but elsewhere in North America the only genera in common with the Montagne Noire, including *Geragnostus*, *Ampyx* and *Pliomerops*, are members of almost ubiquitous groups. The province probably had a considerable extension eastwards as several species of *Taihungshania*, including *T. miqueli*, have been reported from south-western China (Sheng 1958), together with synhomalonotids and asaphids including *Paramegalaspis*. The resemblance of *Hanchungolithus primitivus* to *H. multiseriatus* from this region was discussed earlier, and the Llanvirn age of the Chinese species suggests that *Hanchungolithus* migrated eastwards from the Montagne Noire, but the manner in which the two regions were connected during early Ordovician times is not yet clear. Trilobites of estimated Llandeilo age from a deep borehole in Syria (Stubblefield *in* Sudbury, 1957) include *Colpocoryphe*, whilst my own unpublished researches show that *Dalmanitina*, *Kloucekia* and the trinucleid genus *Marrolithoides* occur in a Caradoc fauna in south-eastern Turkey, so there is no doubt that some Middle Ordovician faunas were widely distributed in the Mediterranean region, but evidence for the lowest Ordovician strata is not yet available.

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EXPLANATION OF PLATES

Most of the trilobites illustrated are in the collections of the British Museum (Natural History) and their numbers are prefixed I., In. or It. Some are in the Geological Institute of the University of Montpellier, whilst the originals of the figured casts of *Geragnostus tullbergi* (Novák) are in the National Museum, Prague. The localities cited for the Landeyran Valley—Le Foulon district are shown in Text-figs. 3 and 5. The specimens were whitened with ammonium chloride before photographing. Photographs by the writer.

PLATE 1

Geragnostus occitanus Howell p. 274

Couches du Landeyran inférieures, locality λ31, hill-side section south-west of Le Foulon.

FIG. 1. Internal mould of dorsal exoskeleton. It. 140. ×8.
FIG. 4. Latex cast showing poorly-defined pygidial axis. It. 143. ×7.
FIGS. 7, 12. Left lateral and plan views of internal mould. It. 146. ×8.
FIG. 10. Latex cast showing anterior margin of pygidium. It. 148. ×7.

Horizon as for Fig. 1. Locality λ32, hill-side section south-west of Le Foulon.

FIG. 2. Latex cast of small individual. It. 141. ×8.
FIG. 3. Internal mould of cephalon. It. 142. ×9.
FIG. 6. Latex cast showing broad pygidial border. It. 145. ×8.
FIGS. 8, 11. Internal mould and latex cast of pygidium and thorax, showing slight difference in definition of pygidial axis. It. 147. ×8.

Horizon as for Fig. 1. Locality λ5, near northern end of Landeyran Valley.

FIGS. 5, 9. Oblique right lateral and plan views of dorsal exoskeleton, an internal mould with cephalon slightly displaced. It. 144. ×7.

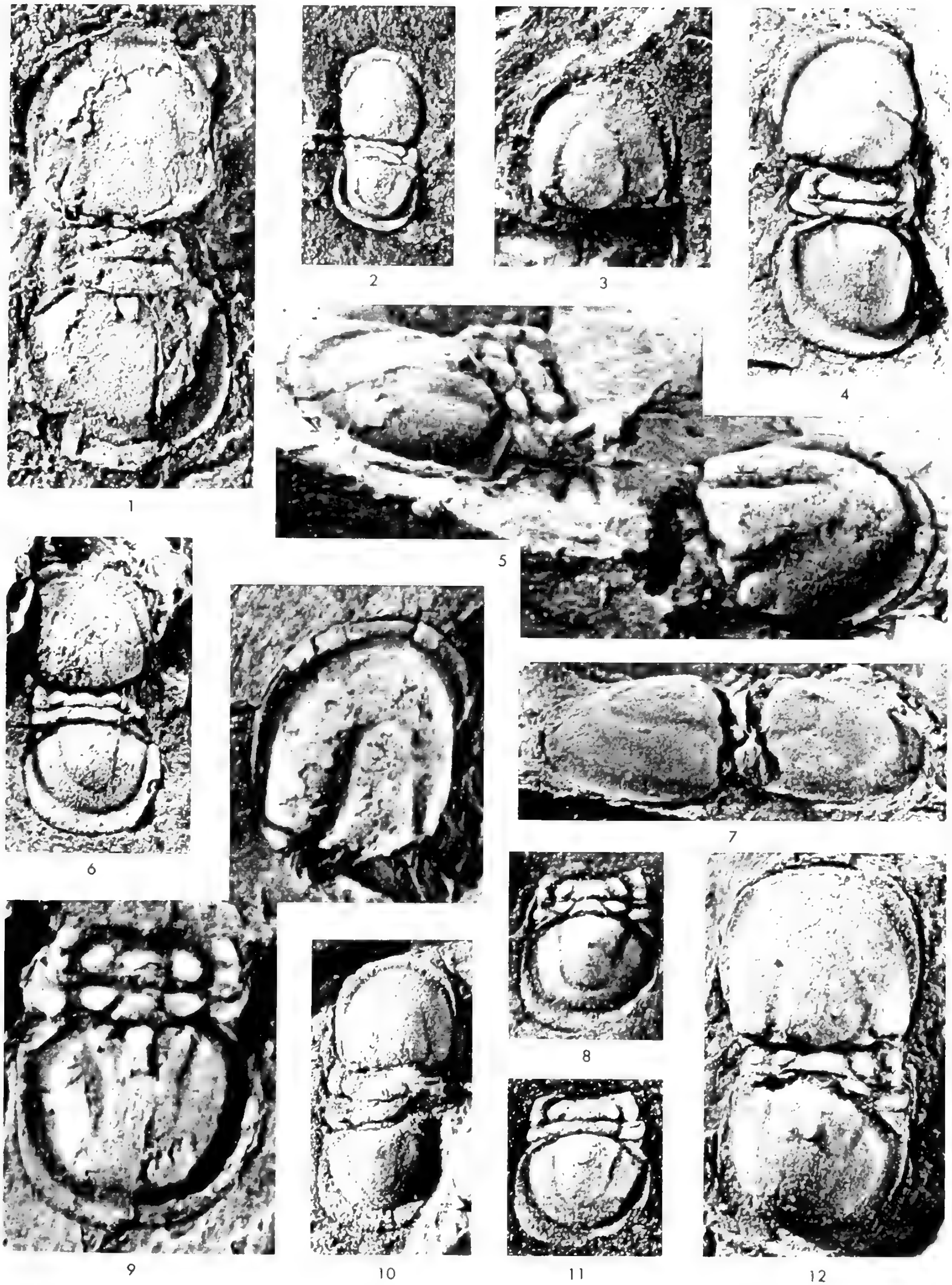
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PLATE 2

Geragnostus occitanus Howell p. 274

Couches du Landeyran inférieures, locality $\lambda 2$,

river bank near northern end of Landeyran Valley.

FIG. 1. Latex cast, FIGS. 2, 3, internal mould. The latter has the second thoracic segment removed to show front of pygidium. In. 57418 (Fig. 1), In. 57419 (Figs. 2, 3). $\times 9$.

FIG. 7. Plan view of internal mould of cranidium. In. 57417. $\times 10$.

Geragnostus tullbergi (Novák) p. 273

Šárka Beds (Llanvirn Series), Šárka, near Prague,
Czechoslovakia.

FIG. 4. Cast of pygidium associated with other specimens of same species in small, siliceous concretion. Original in National Museum, Prague. $\times 4$.

FIG. 9. Enlargement of same pygidium showing poorly-defined tip of axis with median tubercle. $\times 8$.

FIG. 10. Latex cast of associated enrolled individual showing left pleural tips and articulation of thorax. $\times 10$.

Geragnostus mediterraneus Howell p. 277

Horizon and locality as for Fig. 1.

FIGS. 5, 6, 8. Posterior, left lateral and plan views of internal mould of pygidium. In. 57420. $\times 9$.

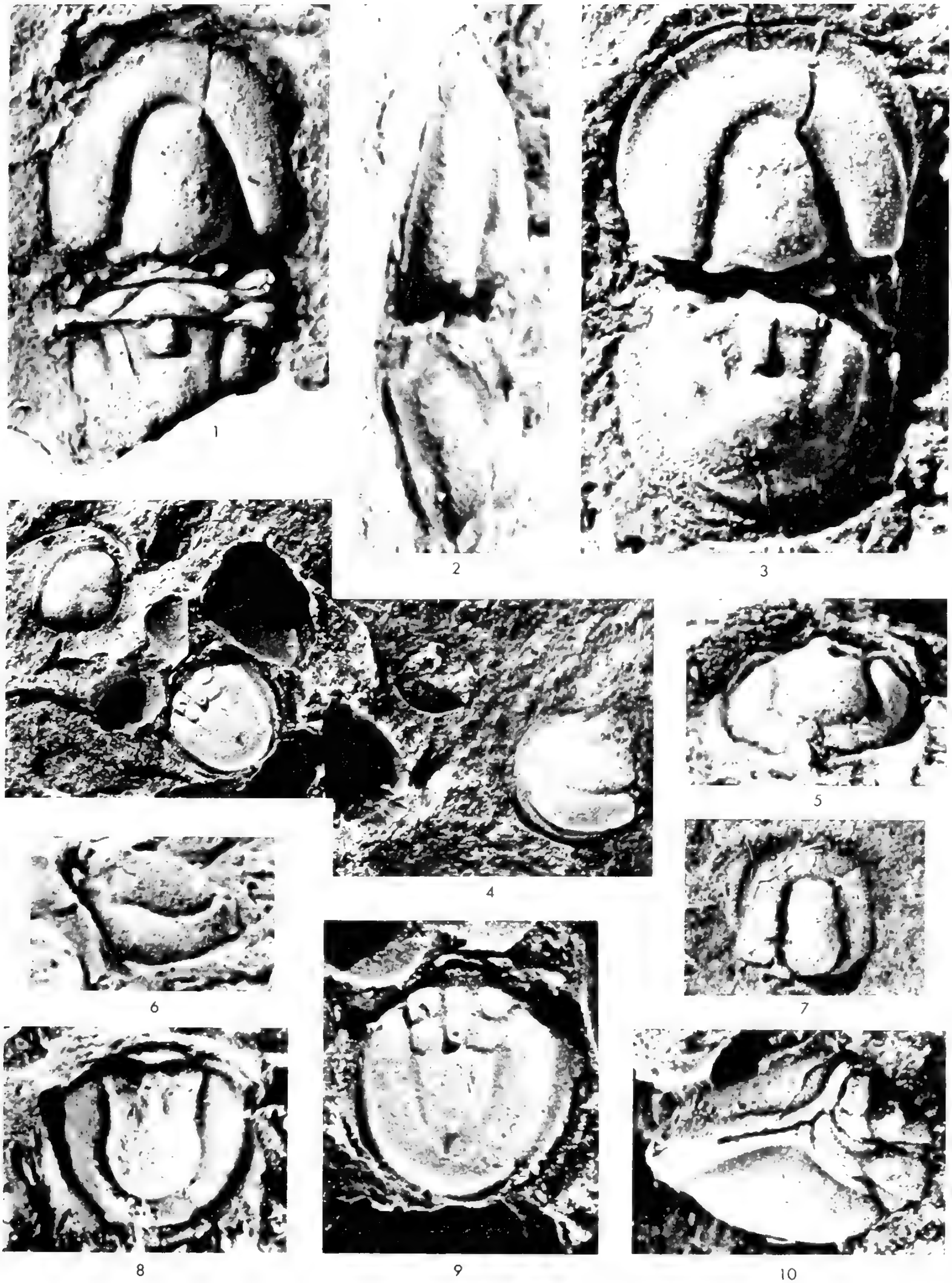
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PLATE 3

Ampyx priscus Thoral p. 279

Couches du Landeyran inférieures, locality $\lambda 32$,
hillside section south-west of Le Foulon.

FIG. 1. External mould of cephalon. It.150*b*. ×6.
FIG. 7. Internal mould of hypostoma. It.150*a*. ×12.

Horizon probably as for Fig. 1. " St. Chinian "
(no precise data).

FIGS. 2, 8. Cast of paralectotype pygidium, University of Montpellier. Original figured Thoral, 1935*a*, pl. 28, fig. 10. Plan and posterior views, ×6.
FIGS. 3, 4, 9. Cast of lectotype cranidium, University of Montpellier. Original figured Thoral 1935*a*., pl. 28, fig. 9. Anterior, left lateral and plan views, ×4.

Horizon probably as for Fig. 1.
" Boutoury ", near Cabrières (no precise data).

FIG. 5. Internal mould of almost complete individual. University of Montpellier. ×5.
Horizon probably as for Fig. 1. Landeyran Valley (no precise data).

FIG. 6. Internal mould, somewhat damaged and abraded. Escot Coll., I.15880. ×5.

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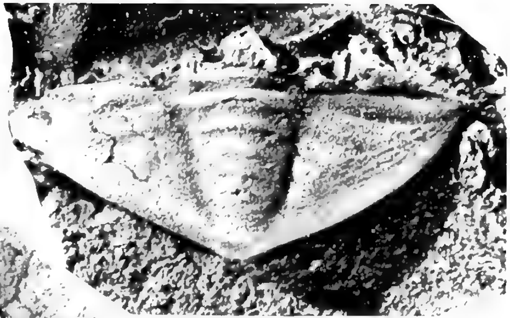

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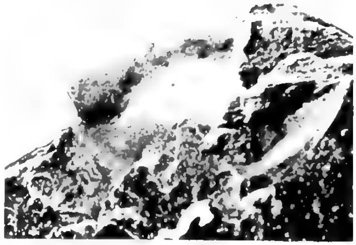

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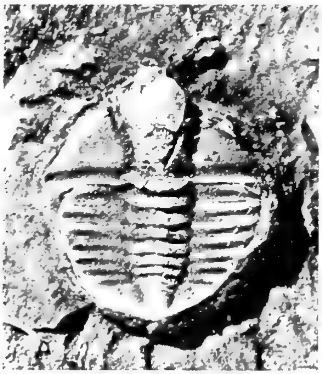

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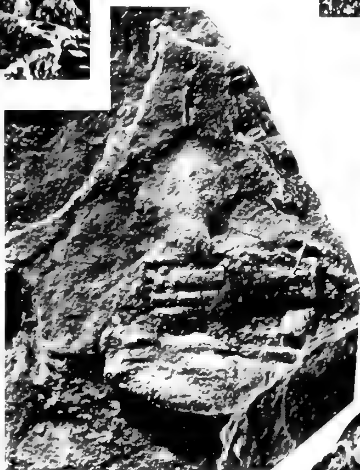

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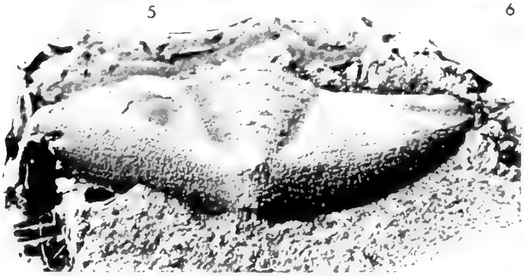

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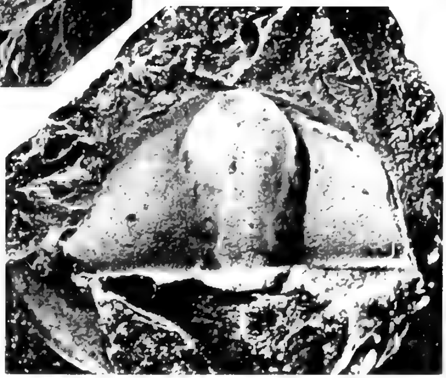

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PLATE 4

Ampyx priscus Thoral p. 279.

Couches du Landeyran inférieures. Locality $\lambda 32$,
hillside section south-west of Le Foulon.

FIG. 1. Two enrolled individuals showing external mould of dorsal side of thorax and ventral side of librigenal spines. Hypostoma preserved as internal mould (for enlargement see Pl. 3, fig. 7). It.150*a*. ×6·5.

FIG. 4. Latex cast of small pygidium with one attached thoracic segment. It.153*b*. ×8.

FIG. 5. Internal mould of cephalon and thorax with external mould of librigenal spines. It.154. ×6·2.

FIG. 6. Latex cast of cranidium. It.155*b*. ×6·2.

Horizon as for Fig. 1.
Locality $\lambda 33$, hillside section south-west of Le Foulon.

FIG. 2. External mould of small cranidium with attached thorax and pygidium. It.151*b*. ×8.

FIG. 3. Internal mould of cranidium. It.152*a*. ×8.

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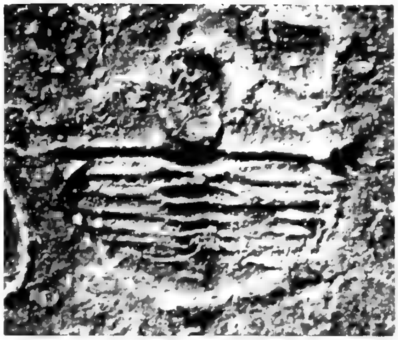

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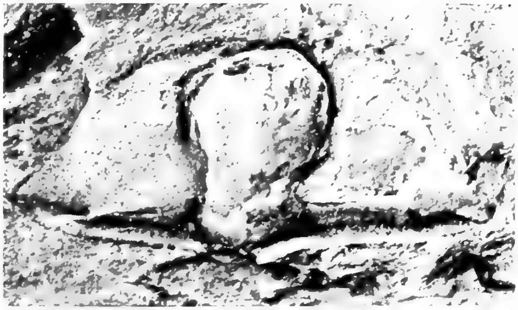

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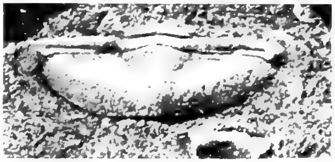

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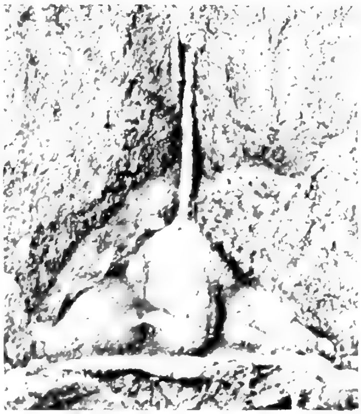

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PLATE 5

Hanchungolithus primitivus (Born) p. 281

Couches du Landeyran supérieures, locality λ16,
near southern end of Landeyran Valley.

FIG. 1. Latex cast of meraspid cephalon showing ocular ridges and alar lobes. In. 56551. ×10.

FIGS, 2, 5. Plan and anterior views of latex cast of dorsal exoskeleton showing, *inter al.*, marginal suture. In. 56534. ×7·5.

FIG. 8. Latex cast of small meraspid cephalon. Note ocular ridges, alar lobes, thick cephalic margin and librigenal spines. In. 58600. ×10.

Horizon as for Fig. 1.

Locality λ20, near southern end of Landeyran Valley.

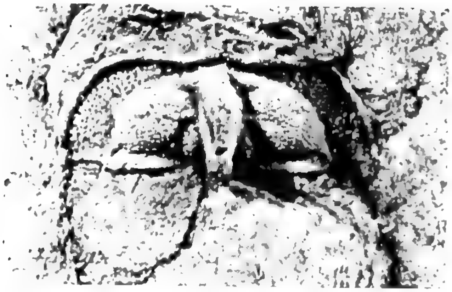
FIG. 3. Internal mould of cephalon showing marginal position of girder. In. 58591. ×9.

FIG. 4. Specimen showing dorsal side of internal mould of cephalic fringe. Centre of cephalon has broken away to show external mould of enrolled thorax. In. 57935. ×8.

FIG. 6. Latex cast of Meraspis (probably Degree 4). In. 58596. ×7.

FIG. 7. Latex cast of two small cephala, the uppermost with well-developed alar lobes. In. 57939. ×10.

FIG. 9. Two individuals showing external mould of dorsal fringe surface and internal mould of thorax. In. 58594. ×4.



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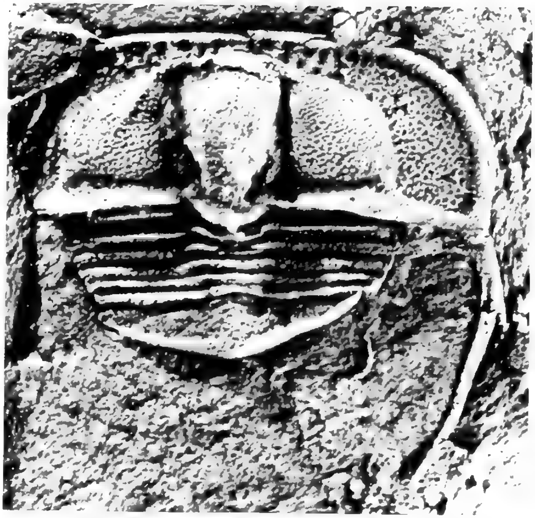

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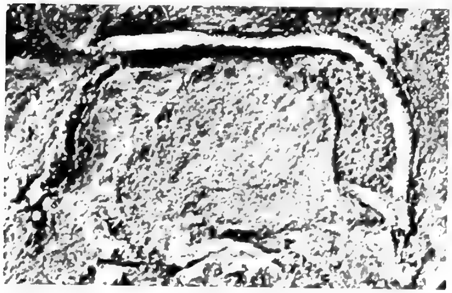

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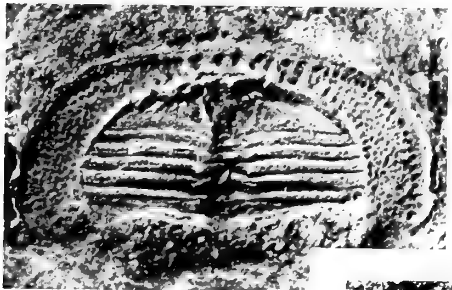

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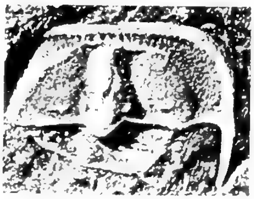

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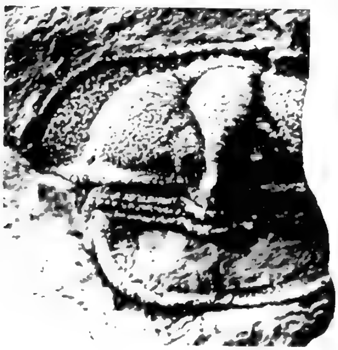

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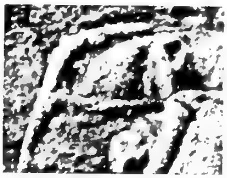

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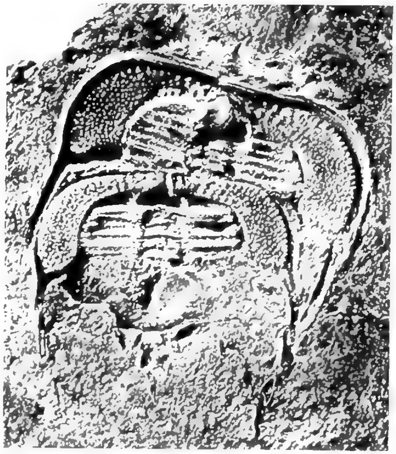

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PLATE 6

Pliomerops escoti (Bergeron) p. 284

Couches du Landeyran inférieures, locality $\lambda 2$,
in north-western bank of river near northern end of Landeyran Valley.

FIGS, 1, 2. Internal mould and latex cast of hypostoma provisionally assigned to the species. It.158. $\times 4 \cdot 5$.

FIG. 3. Latex cast of slightly crushed cranidium. It.159. $\times 4$.

FIG. 9. Latex cast of transitory pygidium, Meraspis, Degree 13. It.161. $\times 6 \cdot 5$.

Horizon as for Fig. 1.
Exact locality in Landeyran Valley unspecified
but probably near the northern end.

FIG. 4. Latex cast of slightly disarticulated dorsal exoskeleton. Escot Coll., I.15877. $\times 3 \cdot 75$.

FIGS. 6, 8, 10. Posterior, oblique right lateral and plan views of internal mould of pygidium. Escot Coll., I.15878. $\times 4 \cdot 5$.

Ceraurinella peregrinus sp. nov. p. 287

Horizon as for Fig. 1. Locality $\lambda 32$, hillside
section south-west of Le Foulon.

FIGS, 5, 7. Plan and left lateral views of latex cast of damaged cranidium. Paratype, It.169. $\times 6 \cdot 5$.

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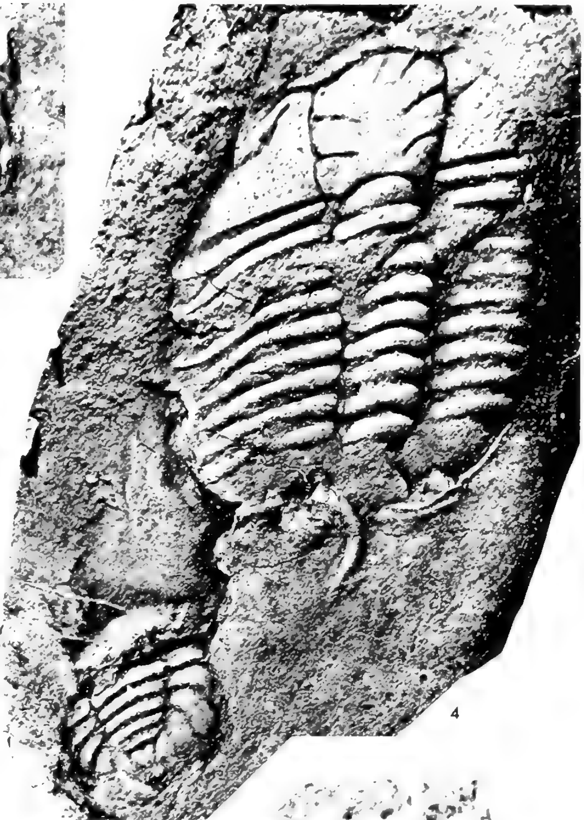

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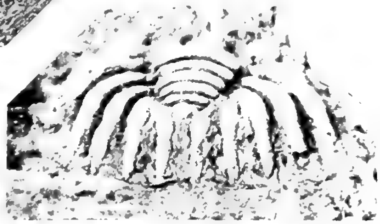

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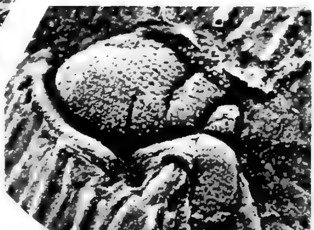

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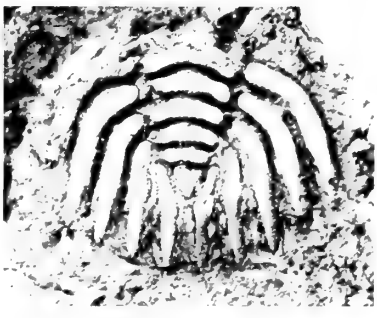

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PLATE 7

Ceraurinella peregrinus sp. nov. p. 287

Couches du Landeyran inférieures, from unspecified locality or localities near Le Foulon.

FIGS. 1, 2, 7. Posterior, right anterolateral and plan views of an internal mould. Holotype, Guiraud Coll., University of Montpellier. $\times 3$.

FIGS. 3, 6. External mould and latex cast of hypostoma of holotype. $\times 8$.

FIG. 4. Latex cast of pygidium and part of thorax. Paratype, Guiraud Collection, University of Montpellier. $\times 3$.

FIGS. 8, 9. Internal mould and latex cast of pygidium, thorax and fragment of cephalon. Paratype, Guiraud Collection, University of Montpellier. $\times 3$.

Horizon as for Fig. 1. Locality $\lambda 2$ in north-western bank of river, near northern end of Landeyran Valley.

FIG. 5. Latex cast of small cranidium. Paratype, It. 160. $\times 6$.

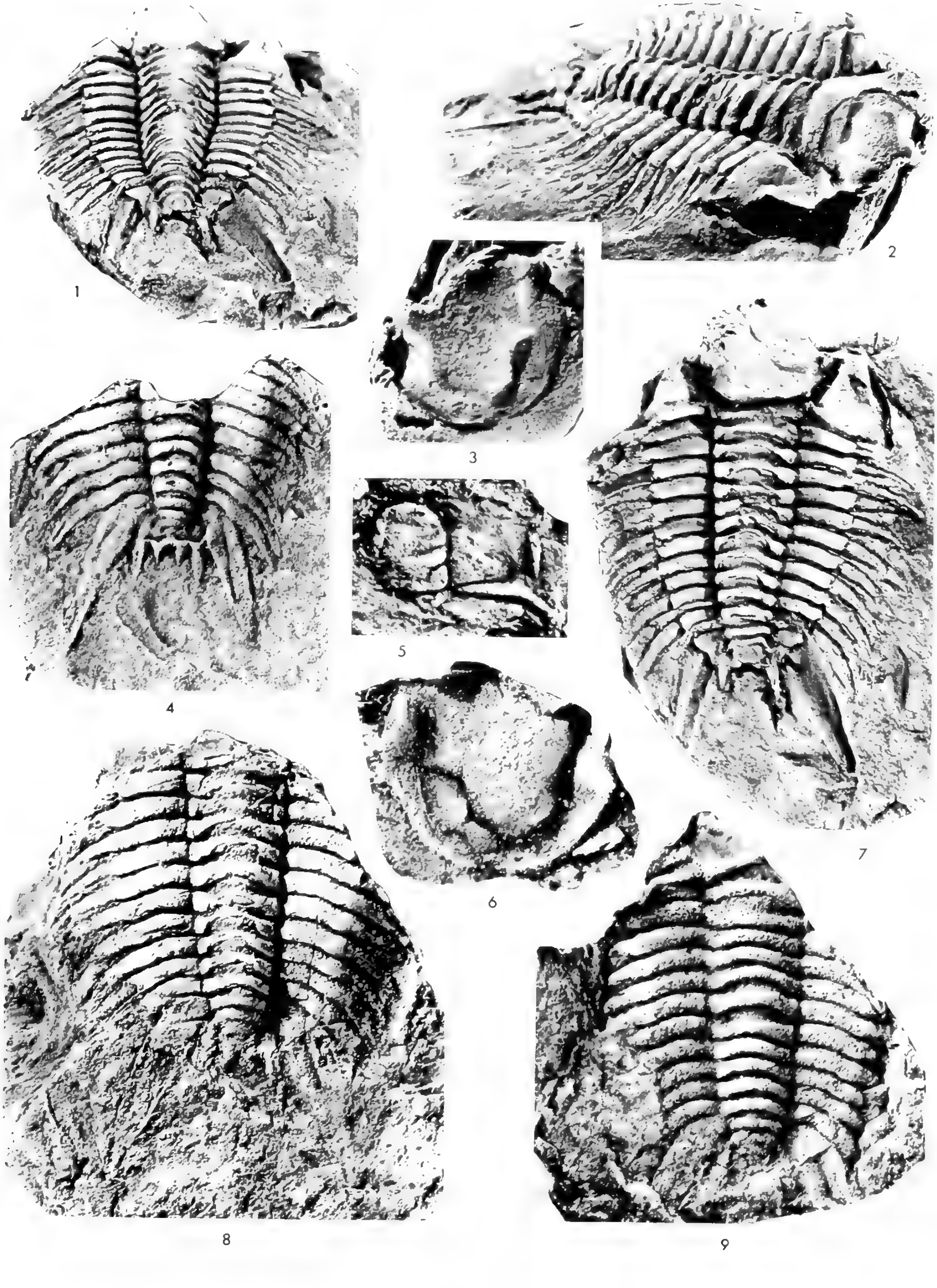
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PLATE 8

Ormathops borni sp. nov. p. 292

Couches du Landeyran supérieures, locality $\lambda 16$,
near southern end of Landeyran Valley.

FIGS. 1, 6. Plan and left lateral views of internal mould of dorsal exoskeleton. Paratype, In.56620. ×7.

FIGS. 2–4. Anterior, left lateral and plan views of internal mould of cephalon. Paratype, In.57448. ×8.

FIG. 7. Left lateral view of latex cast of damaged cephalon showing eye facets, cheek and facial suture. Paratype, In.56614. ×10.

FIG. 8. Internal mould of small individual Paratype, In.56557. ×8.

Couches du Landeyran inférieures, locality $\lambda 33$,
hillside section south-west of Le Foulon.

FIG. 5. Plan view of cephalon, an internal mould. It.285. ×6.

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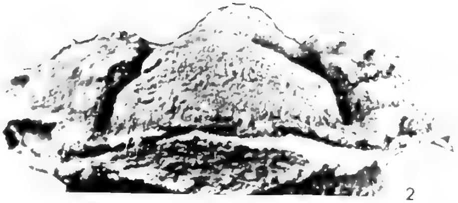

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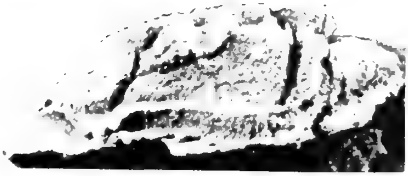

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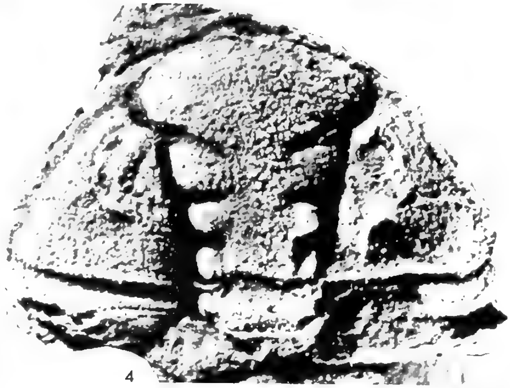

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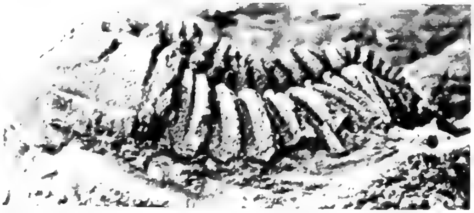

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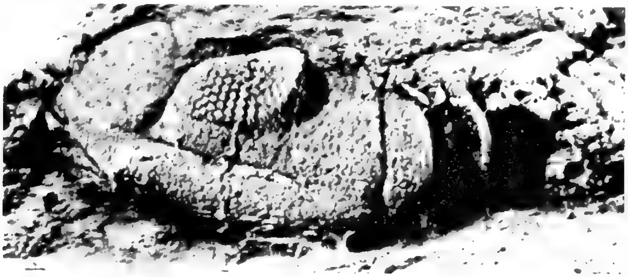

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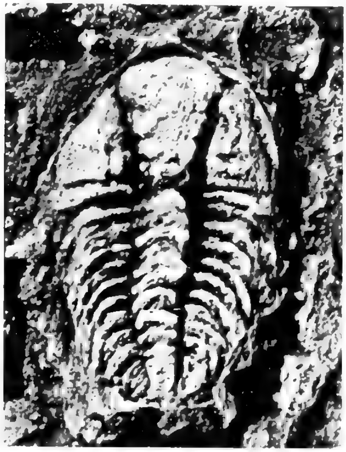

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PLATE 9

Ormathops borni sp. nov. p. 292

Couches du Landeyran supérieures, locality $\lambda 16$,
near southern end of Landeyran Valley.

FIG. 1. Internal mould of cephalon showing impression of doublure. Paratype, In.57772. ×5·5.

FIG. 2. Latex cast of small hypostoma. Paratype, In.56613. ×15.

FIG. 3. Internal mould of small cranidium. Paratype, In.56609. ×7.

FIGS. 4, 9, 10. Anterior, left lateral and plan views of holotype cephalon, an internal mould. In.57447. ×5·5.

FIGS. 5, 12. Latex cast of pygidium. Paratype, In.57898. ×6·5.

FIG. 11. Latex cast showing cephalic border. Paratype, In.57953. ×5.

FIG. 13. Latex cast of small cephalon showing well-developed fixigenal spine. Paratype, In.57446. ×12.

Horizon as for Fig. 1.
Locality $\lambda 17$, near southern end of Landeyran Valley.

FIG. 7. Internal mould of small individual showing fixigenal spine and cephalic test. In. 56588. ×6.

Couches du Landeyran inférieures, locality $\lambda 33$,
hillside section south-west of Le Foulon.

FIGS. 6, 8. Internal mould and latex cast of slightly compressed pygidium. It.286. ×6.

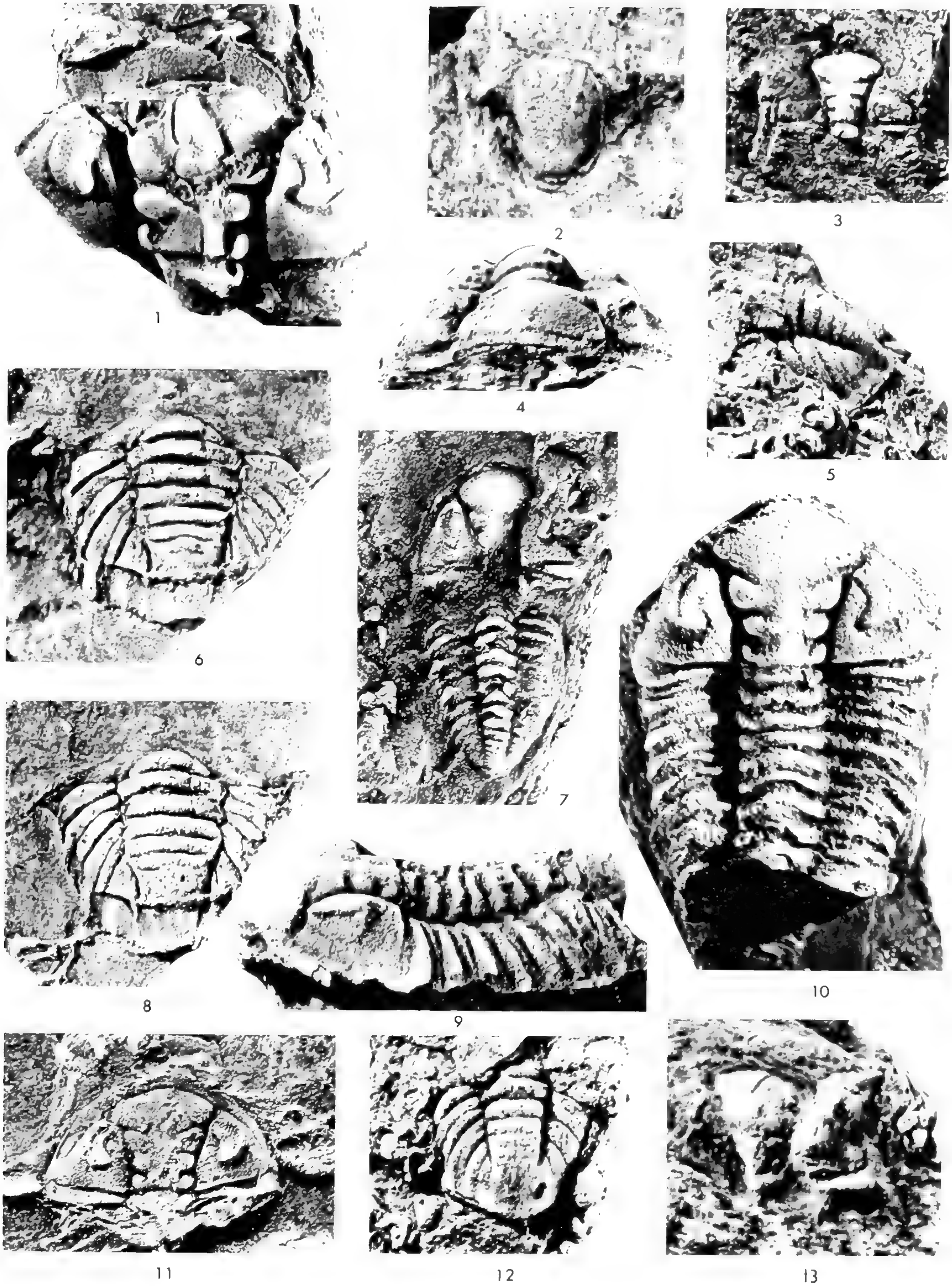
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PLATE 10

Prionocheilus matutinus sp. nov. p. 300

Couches du Landeyran inférieures, locality λ2,
near northern end of Landeyran Valley.

FIG. 1. Internal mould of cranidium, thorax and part of pygidium. Paratype, It.162. ×4·5.

FIG. 2. Latex cast of librigena showing small ventral spines. Paratype, In.57486*b*. ×10.

FIG. 3. Latex cast of small pygidium with fragment of thorax. Paratype, In.57430. ×9.

FIG. 6. Latex cast of small cranidium. Paratype, It.164. ×11.

FIG. 7. Latex cast of incomplete cranidium, showing paraglabellar areas and granulated test. Holotype, In.57434*b*. ×6·5.

Bathycheilus gallicus Dean p. 298

Horizon as for Fig. 1. Unspecified locality near Le Foulon.

FIG. 4. Internal mould of dorsal exoskeleton. Guiraud Coll., University of Montpellier. ×4·5.

Horizon and locality as for Fig. 1.

FIG. 8. Internal mould of hypostoma. In.57482. ×6·5.

FIG. 12. Latex cast of fragmentary cephalon. In.57483. ×5·3.

Horizon as for Fig. 1.
Locality λ32, hillside section south-west of Le Foulon.

FIG. 9. Latex cast of two cranidia. It.165. ×4·5.

Horizon as for Fig. 1.
Locality λ33, hillside section south-west of Le Foulon.

FIG. 10. Latex cast of small cranidium (?Meraspis). It.166. ×12.

FIG. 11. Internal mould of cranidium, probably small Holaspis. It.167. ×4·5.

Colpocoryphe thorali sp. nov. p. 304

Horizon and locality as for Fig. 9.

FIG. 5. Latex cast of Meraspis cranidium and thorax. Paratype, It.168. ×10.

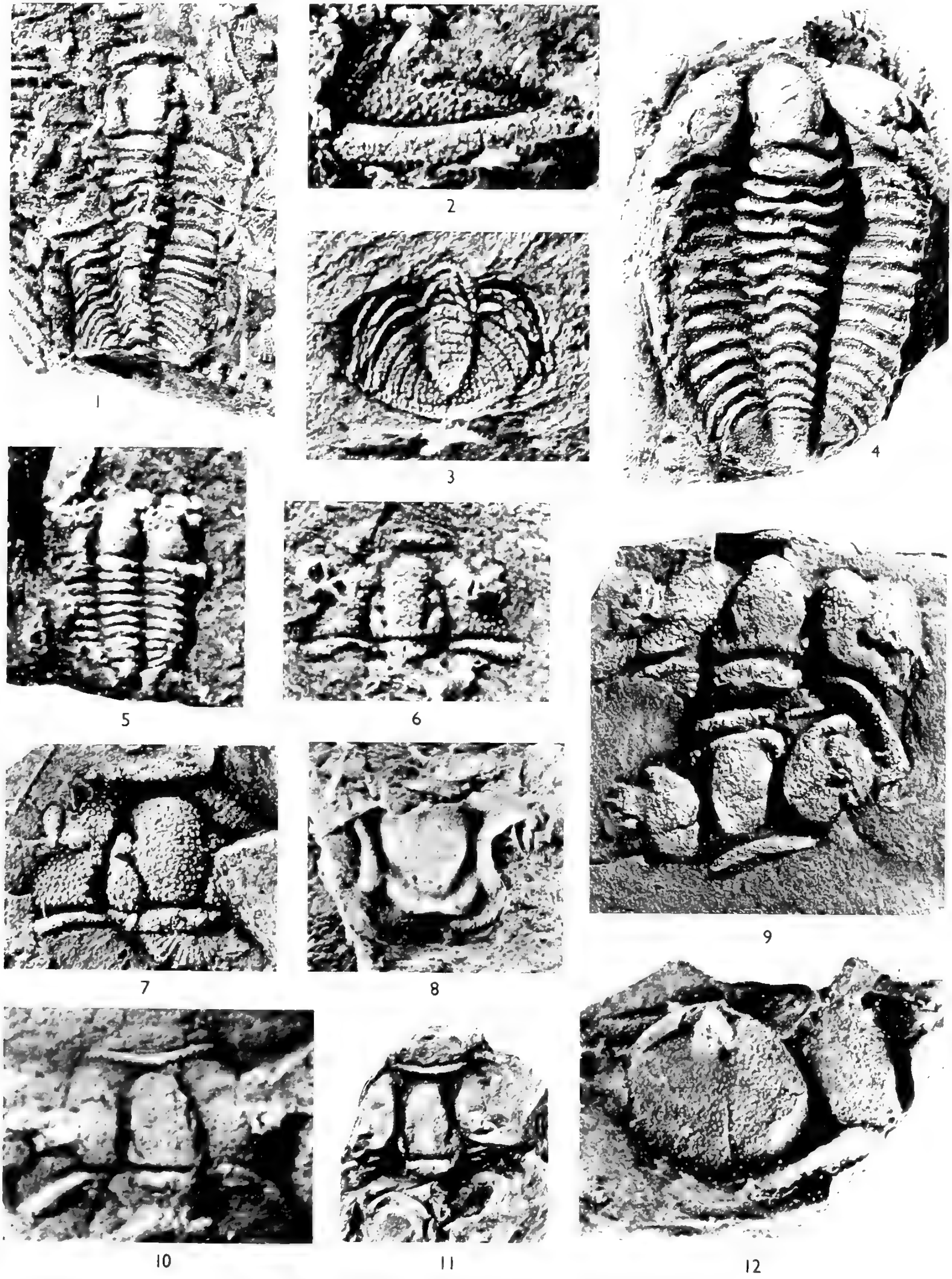
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PLATE 11

Colpocoryphe thorali sp. nov. p. 304

Couches du Landeyran supérieures, locality λ16, near southern end of Landeyran Valley.

FIG. 1. Latex cast of small pygidium. Paratype, In.57622. ×9.

Couches inférieures du Landeyran, locality λ32, hillside section south-west of Le Foulon.

FIGS. 2, 10. Internal mould of cephalon. It.170, ×4·25.

FIGS. 3, 8. External mould of exoskeleton with internal mould of hypostoma in place. It.171. Fig. 3, ×8. Fig. 8, ×5.

Horizon as for Fig. 2.
Locality λ31, hillside section south-west of Le Foulon.

FIG. 4. Latex cast of small, partially disarticulated exoskeleton. It.172. ×8.

Horizon as for Fig. 1.
Locality λ19, near southern end of Landeyran Valley.

FIG. 5. Internal mould of cranidium of small Meraspis. In.57510. ×14.
FIG. 7. Latex cast of cranidium of small Meraspis. In.57498. ×12.
FIG. 9. Latex cast of small individual (? Meraspis Degree 11). In.57504. ×14.

Horizon as for Fig. 1.
Locality λ20, near southern end of Landeyran Valley.

FIG. 6. Internal mould of small, slightly compressed cranidium. Paratype,In.57586. ×6.

PLATE 11

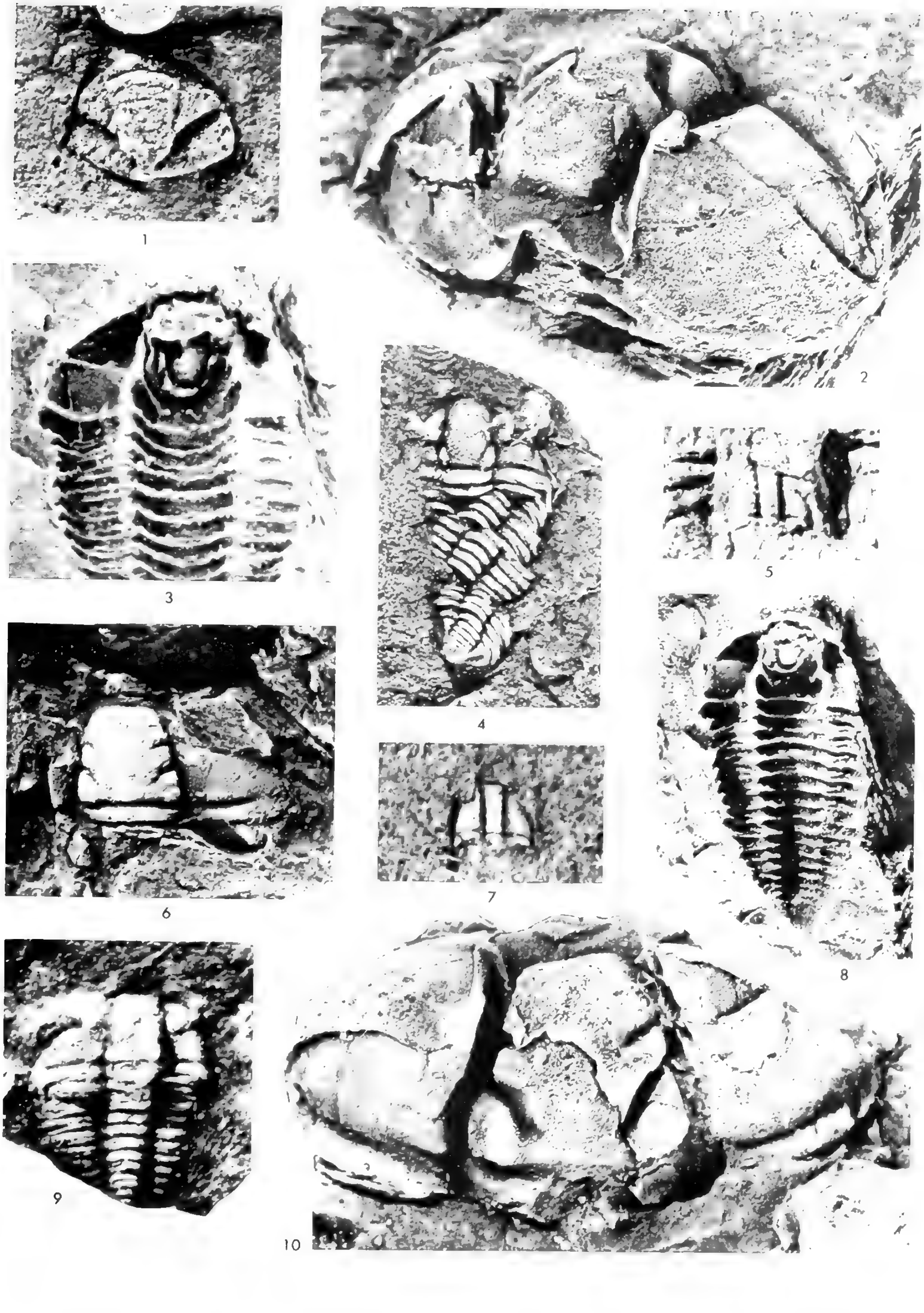

PLATE 12

Colpocoryphe thorali sp. nov. p. 304

Couches du Landeyran supérieures, locality λ20,
near southern end of Landeyran Valley.

FIG. 1. Latex cast of whole exoskeleton. Paratype, In. 57552. ×4.
FIG. 4. Internal mould of small pygidium. In. 57594. ×12.

Horizon as for Fig. 1.
Locality λ16, near southern end of Landeyran Valley.

FIGS. 2, 6, 9. Left lateral, anterior and plan views of latex cast of cephalon. Holotype, In. 56654. ×6.
FIG. 3. Latex cast of hypostoma. Paratype, In. 57438. ×10.

Couches du Landeyran inférieures, locality λ32,
hillside section south-west of Le Foulon.

FIGS. 5, 8. Internal mould of cephalon and part of thorax. It. 173. ×4.

Horizon as for Fig. 5.
Locality λ2, near northern end of Landeyran Valley.

FIG. 7. Latex cast of small exoskeleton (? Meraspis Degree 12). It. 174. ×4·5.

Horizon as for Fig. 1.
Locality λ19, near southern end of Landeyran Valley.

FIG. 10. Internal mould of right librigena showing visual surface of eye. In. 57502. ×10.
FIG. 11. Latex cast of small pygidium with six attached thoracic segments. In. 57516. ×6.

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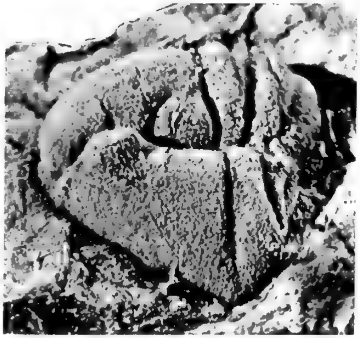

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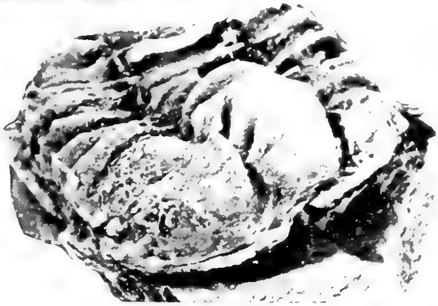

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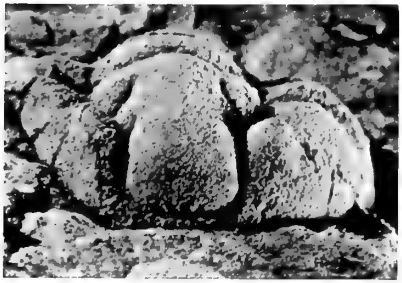

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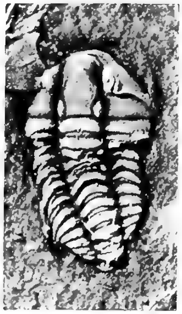

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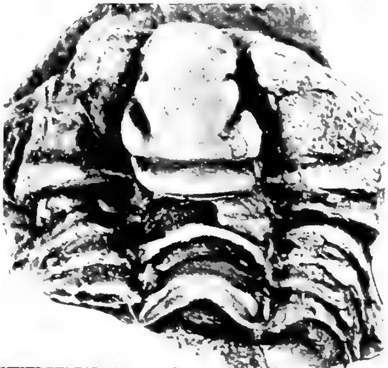

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PLATE 13

Neseuretus antetristani sp. nov. p. 310

Couches du Landeyran supérieures, locality λ20, near southern end of Landeyran Valley.

FIG. 1. Internal mould of pygidium. Paratype, In. 57478. ×6.

Horizon as for Fig. 1.
Locality λ17, near southern end of Landeyran Valley.

FIGS. 2, 6, 7. Plan, left lateral and posterior views of internal mould of pygidium. Paratype, In. 57473. ×2.

FIGS. 3, 5. Plan, anterior and right lateral views of latex cast of cranidium. Holotype, In. 57475. ×2. Note facial suture, with rostral plate in position.

FIG. 8. Internal mould of incomplete cranidium, showing lobation of glabella, and left ocular ridge. Paratype, In. 56682. ×1·5.

FIG. 9. Internal mould of cranidium. Paratype, In. 57474. ×1·4.

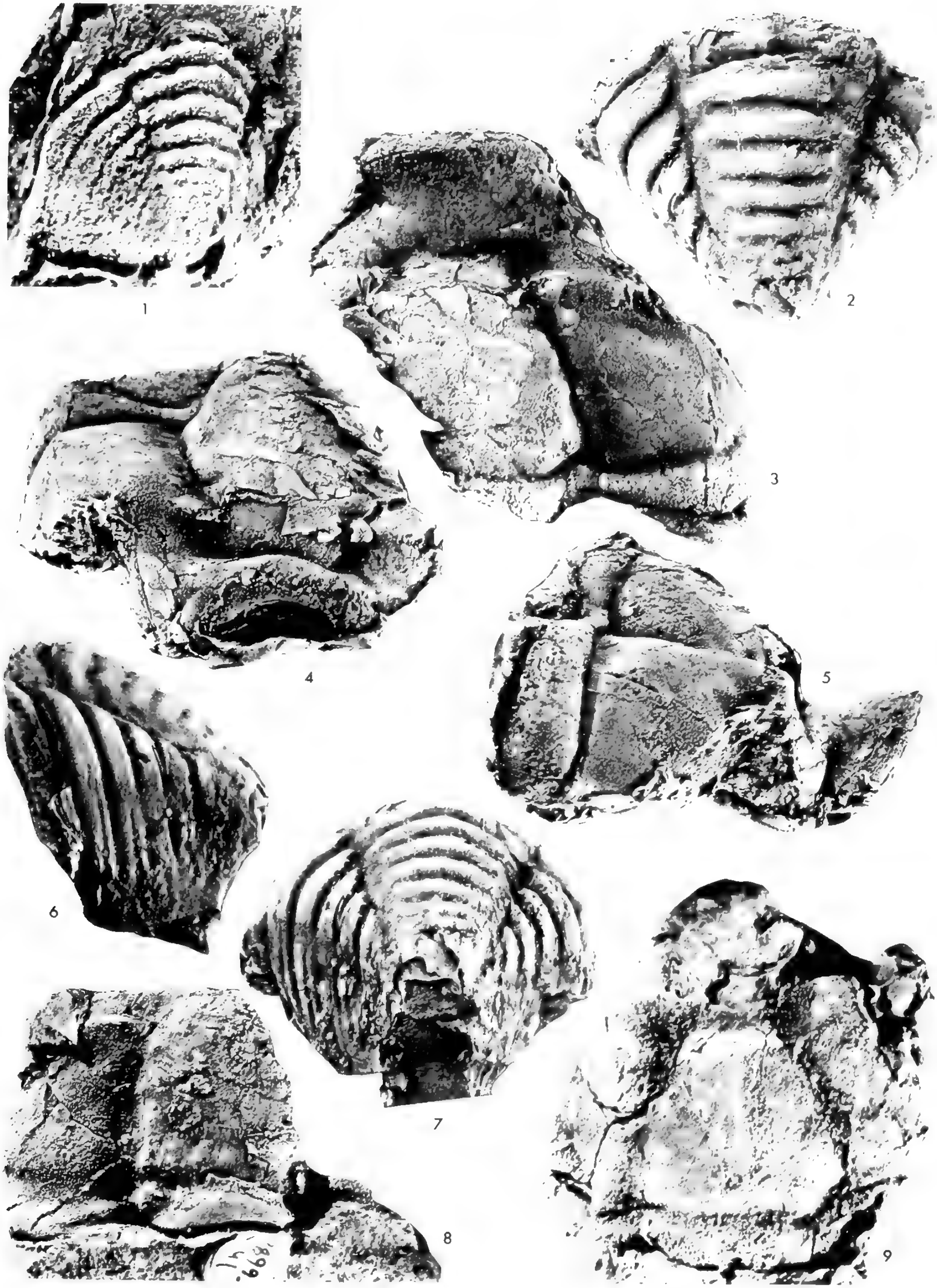
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PLATE 14

Neseuretus arenosus sp. nov. p. 313

Couches du Landeyran inférieures
from loose concretion found 400 metres north-east of l'Escougoussou.

FIGS. 1, 4, 8. Internal mould of pygidium. Paratype, In.57751. ×4.

Couches du Foulon,locality λ7, about 500 metres south-west of Upper Bridge, Landeyran Valley.

FIG. 5. Internal mould of pygidium. Paratype, In.57752. ×4.
FIGS. 7, 9, 11. Latex cast of cranidium. Holotype, In.57754. ×5.

Neseuretus attenuatus (Gigout) p. 317

Ordovician : Llanvirn? Series.
Jbel Zini, near Tilemsoun, Anti Atlas, Morocco.

FIGS. 2, 6, 12. Internal mould of topotype cranidium. Destombes Coll., It.244. ×3.

Platycoryphe convergens sp. nov. p. 318

Couches du Landeyran supérieures, locality λ19,
near southern end of Landeyran Valley.

FIGS. 3, 10, 13. Anterior, left lateral and plan views of internal mould of cranidium. Holotype, In.57756. ×7.

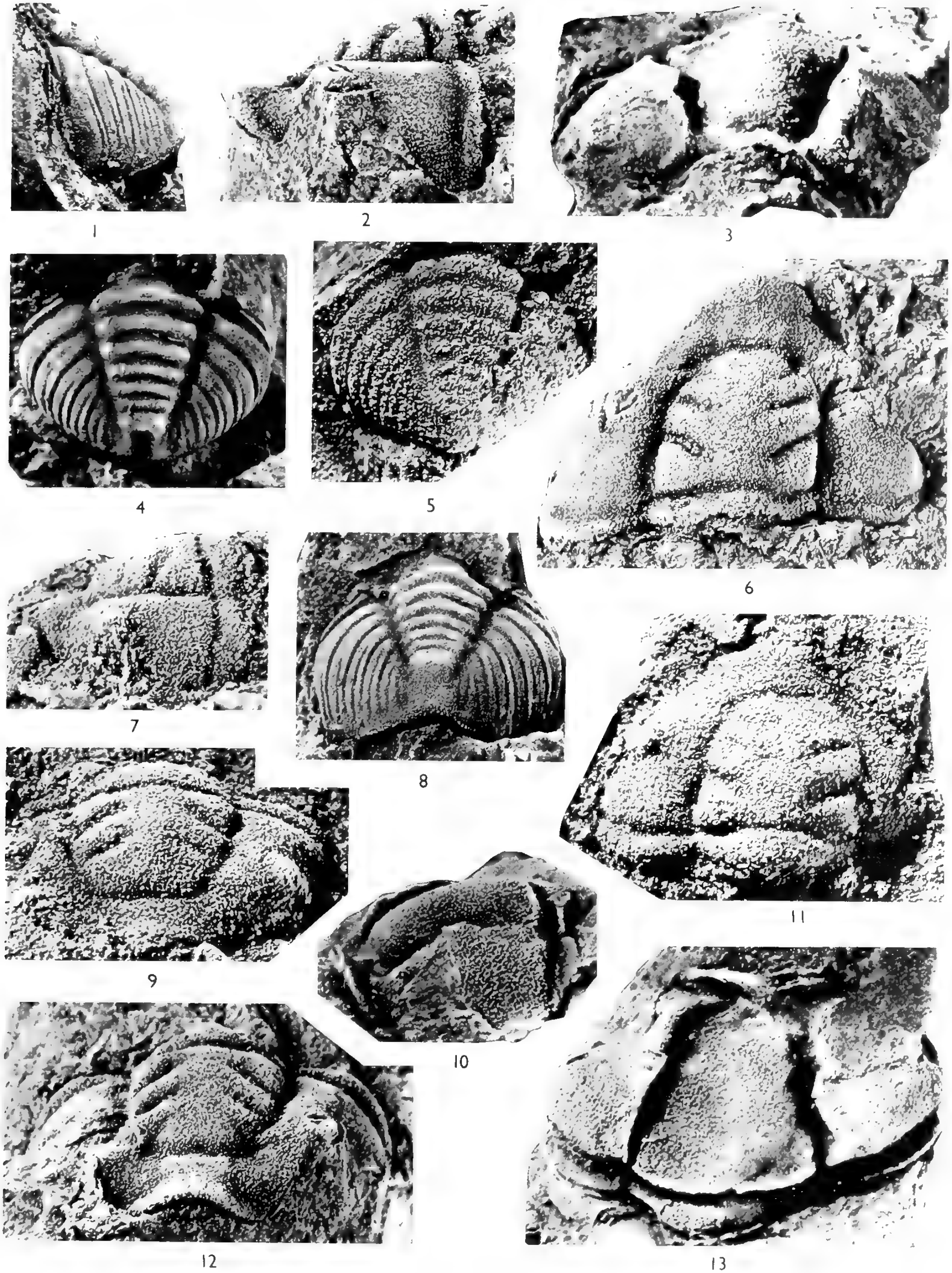
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PLATE 15

Proetid gen. et sp. indet. p. 338

Horizon probably Couches du Landeyran inférieures ;
" Le Foulon ", exact locality unspecified.

FIGS. 1, 7. Plan and anterior views of internal mould of cranidium. University of Montpellier. $\times 3$.

Niobella cf. ***lignieresi*** (Bergeron) p. 329

Couches du Landeyran inférieures,
locality $\lambda 4$, near northern end of Landeyran Valley.

FIG. 2. Latex cast of cranidium. It.252. $\times 1 \cdot 5$.

Horizon as for Fig. 2.
Locality $\lambda 5$, near northern end of Landeyran Valley.

FIG. 4. Internal mould of pygidium. In.57744. $\times 1 \cdot 5$.

Niobella? sp. p. 329

Horizon as for Fig. 2.
Locality $\lambda 2$, near northern end of Landeyran Valley.

FIG. 3. Latex cast of anterior portion of cranidium. It.253. $\times 1 \cdot 5$.

Megistaspis (***Ekeraspis***)***?*** sp. p. 324

Couches du Landeyran supérieures,
locality $\lambda 16$, near southern end of Landeyran Valley.

FIGS. 5, 6. Posterior and plan views of internal mould of pygidium. In.56666. $\times 2$.

Horizon as for Fig. 5.
Locality $\lambda 19$, near southern end of Landeyran Valley.

FIG. 8. Internal mould of pygidium. It.259. $\times 2$.

Niobella fourneti (Thoral) p. 328

Horizon and locality as for Fig. 1.

FIG. 9. Internal mould of cranidium. University of Montpellier. $\times 3$.

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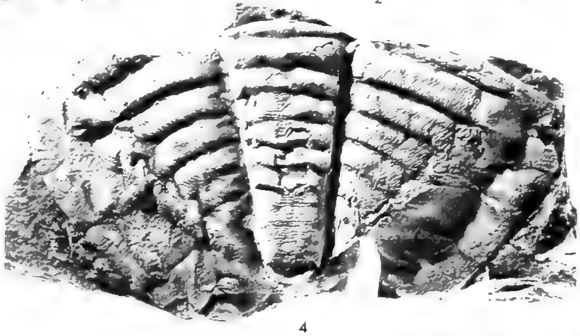

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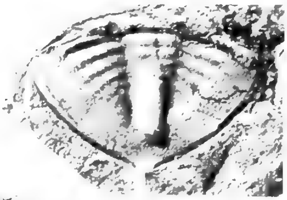

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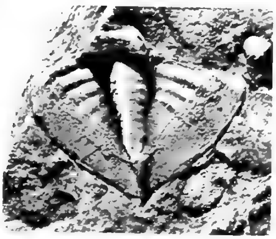

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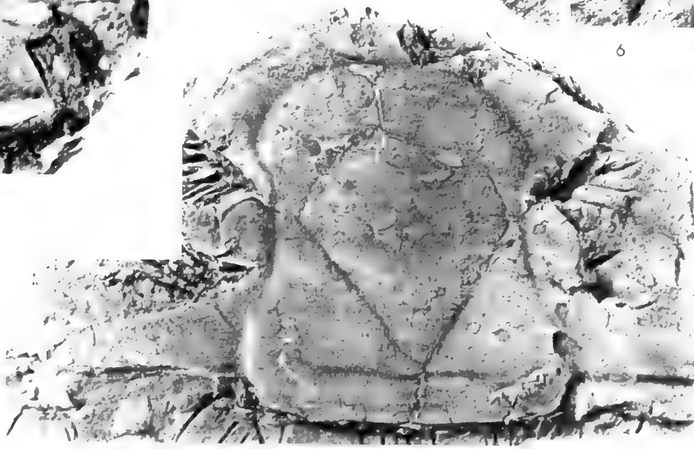

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PLATE 16

Taihungshania landayranensis (Thoral) p. 331

Schistes de Setso, Ruisseau de Setso,
about 1500 metres west-south-west of Upper Bridge.

FIG. 1. External mould of typical cranidium. Matte Coll., University of Montpellier. ×2.
FIG. 7. Internal mould of pygidium. Collection as above. ×2.

***Megistaspis* (*Ekeraspis*)** sp. p. 323

Couches du Landeyran inférieures,
locality λ30, hillside section south-west of Le Foulon.

FIG. 2. Internal mould of small cranidium. It.254. ×6.

Horizon as for Fig. 2.
Locality λ4, near northern end of Landeyran Valley.

FIG. 9. Internal mould of cranidium. In.57682. ×1·5.

Couches du Landeyran supérieures,
locality λ16, near southern end of Landeyran Valley.

FIG. 10. Internal mould of cranidium. In.57741. ×1·5.

Taihungshania miqueli (Bergeron) p. 331

Arenig Series, La Maurerie,
near Prades-sur-Vernazobres, east of St. Chinian.

FIGS. 3, 4. Plan and posterior views of internal mould of pygidium. It.427. ×3.

Basiliella mediterranea sp. nov. p. 320

Horizon as for Fig. 2.
Locality λ31, hillside section south-west of Le Foulon.

FIG. 5. Enlargement showing hypostoma in place. Paratype, It.257. ×4.

Taihungshania sp. p. 332

Horizon as for Fig. 10.
Locality λ19, near southern end of Landeyran Valley.

FIGS. 6, 8. Oblique left lateral and plan views of internal mould of cranidium. In.57750. ×1·5.

Megistaspis (s.l.) sp. p. 324

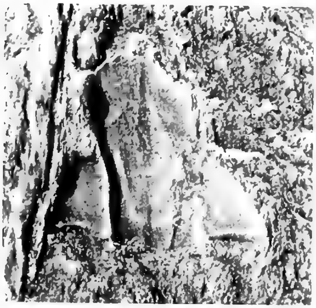
Couches du Landeyran, exact horizon uncertain.
Landeyran Valley, locality not specified.

FIG. 11. Internal mould of incomplete, large hypostoma. University of Montpellier. ×1.

***Megalaspidella* (*Megalaspidella*)** sp. p. 324

Horizon as for Fig. 10.
Locality λ20, near southern end of Landeyran Valley.

FIG. 12. Internal mould of small cephalon. In.57719. ×5.



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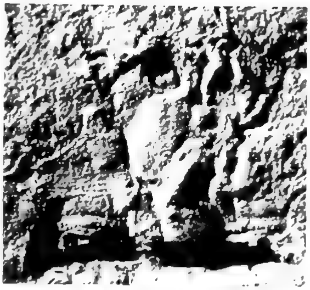

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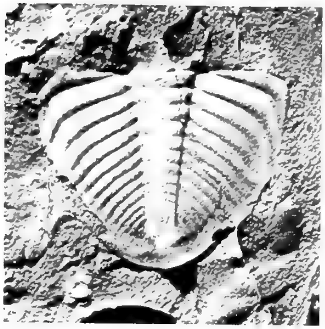

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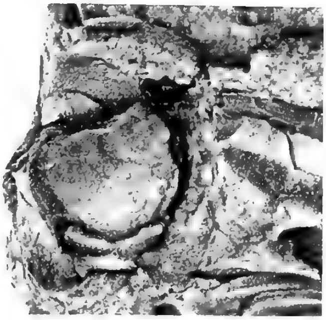

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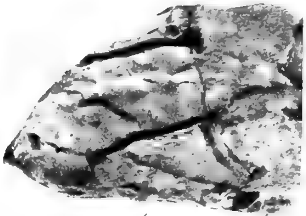

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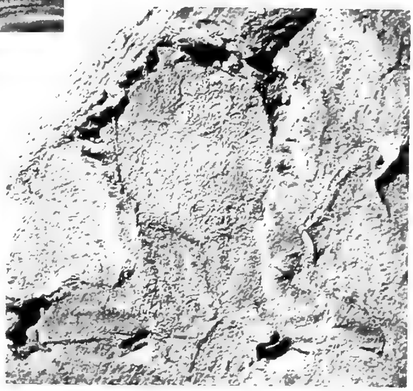

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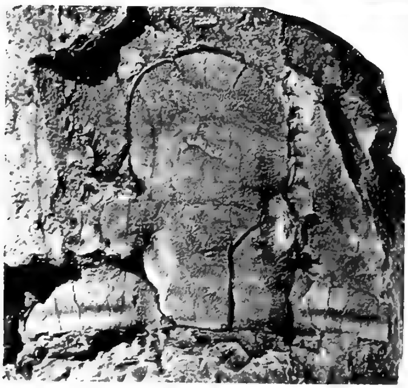

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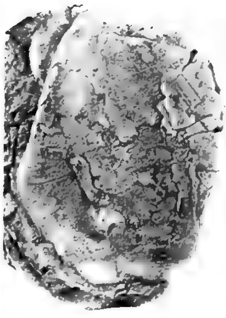

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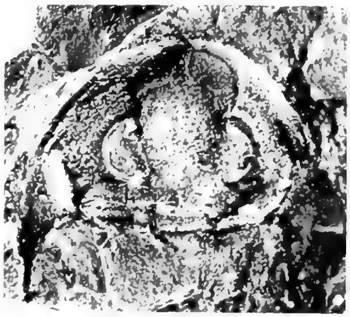

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PLATE 17

Basiliella mediterranea sp. nov. p. 320

Couches du Landeyran supérieures,
locality λ21, near southern end of Landeyran Valley.

FIGS. 1, 4. Plan and anterior views of internal mould of cranidium. Holotype, It. 399. ×4.

Horizon as for Fig. 1.
Locality λ17, near southern end of Landeyran Valley.

FIG. 3. Internal mould of cranidium. Paratype, In. 56847. ×4.
FIGS. 11, 13. Posterior and plan views of internal mould of pygidium. Paratype. In. 56856. ×1·5.

Couches du Landeyran inférieures,
locality λ31, hillside section south-west of Le Foulon.

FIG. 8. Internal mould of incomplete dorsal exoskeleton. Paratype, It. 257. ×1·5.

Horizon as for Fig. 1.
Locality λ8, eastern side of Landeyran Valley.

FIG. 12. Latex cast of incomplete pygidium. Paratype, It. 260. ×3.

Basiliella sp. p. 322

Horizon and locality as for Fig. 3.

FIG. 2. Internal mould of incomplete hypostoma. In. 56844. ×1·8.
FIG. 6. Internal mould of hypostoma. In. 57742. ×3.

?Basiliella mediterranea sp. nov. p. 322

Horizon as for Fig. 8.
Locality λ32, hillside section south-west of Le Foulon.

FIG. 9. Latex cast of hypostoma. It. 269. ×2·5.

Paramegalaspis sp. p. 326

Horion as for Fig. 8.
Locality λ30, hillside section south-west of Le Foulon.

FIG. 5. Latex cast of Meraspis, Degree 3. It. 264. ×14.
FIG. 14. External mould of Meraspis, Degree 4. It. 265. ×14.
FIG. 15. Internal mould of Meraspis, Degree 6. It. 263. ×14.

Horizon as for Fig. 1.
Locality λ16, near southern end of Landeyran Valley.

FIG. 10. Latex cast of Meraspis, Degree 7. In. 57740. ×7.

Megalaspidella sp. (**_Megalaspidella_**) p. 324

Horizon as for Fig. 8.
Locality λ33, hillside section south-west of Le Foulon.

FIG. 7. Internal mould of hypostoma. It. 268. ×2·5.

Ogygiocaris sp. p. 330

Horizon and locality as for Fig. 9.

FIG. 16. Internal mould of fragmentary pygidium. It. 256. ×1·5.

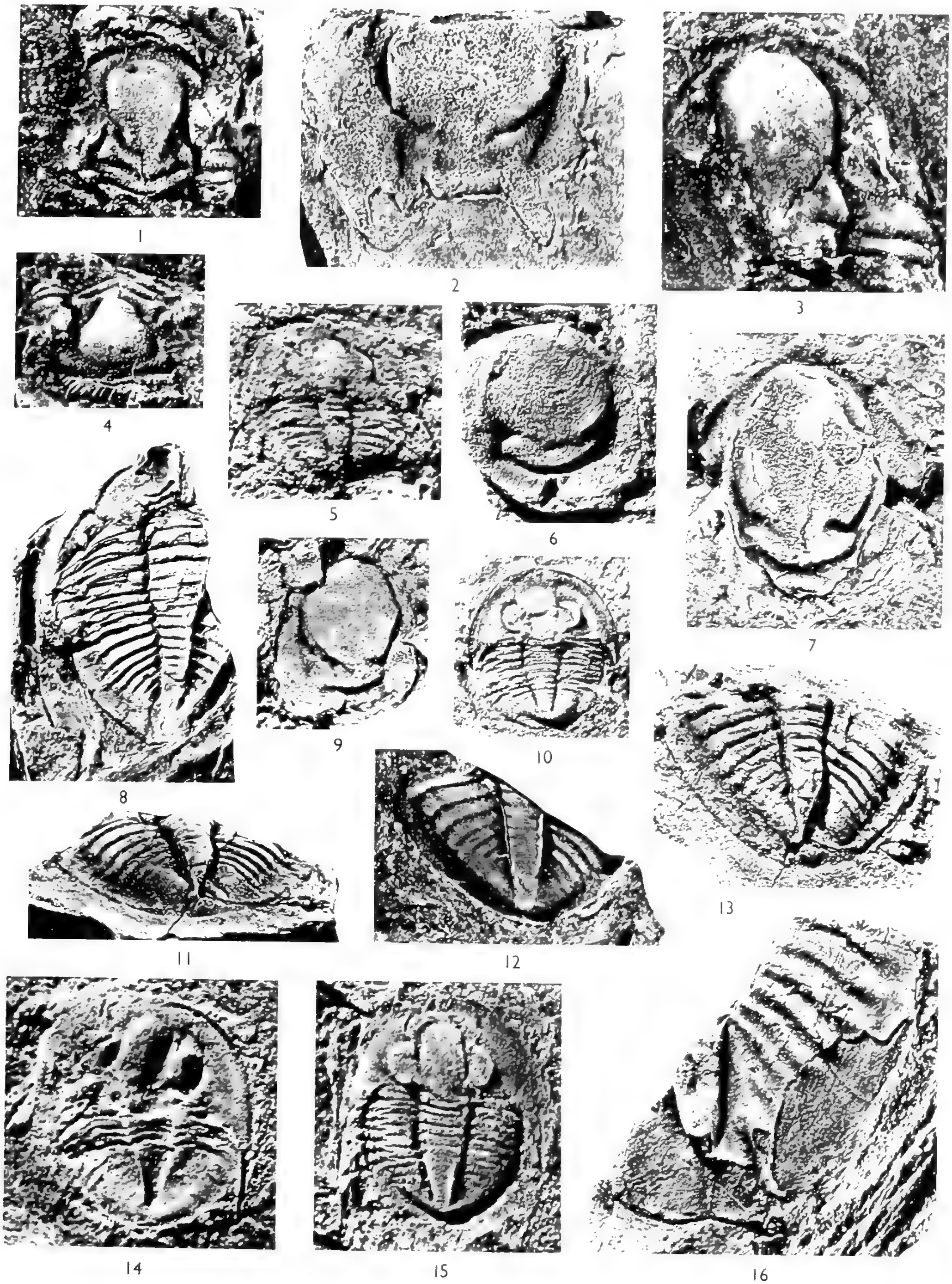
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PLATE 18

Paramegalaspis* cf. *frequens Thoral p. 325

Couches du Landeyran, exact horizon uncertain,
found loose in vicinity of locality λ17, near southern end of Landeyran Valley.

FIGS. 1, 3, 8. Left lateral, anterior, and plan views of cranidium. Figs. 1, 3, internal moulds, Fig. 8, latex cast. It.271. ×1·5.

Probably Couches du Landeyran inférieures
near locality λ4, northern end of Landeyran Valley.

FIGS. 2, 10, 13. Posterior, left lateral, and plan views of pygidium, an internal mould. In.57681. ×1·5.

Symphysurus sabulosus sp. nov. p. 322

Couches du Foulon,
locality λ7, south-west of Upper Bridge, Landeyran Valley.

FIGS. 4, 5, 7. Right lateral, anterior, and plan views of internal mould of cranidium. Holotype. In.57729. ×7.

FIG. 6. Internal mould of cranidium. Paratype, In.57730. ×10.

Paramegalaspis sp. p. 326

Horizon and locality as for Fig. 4.

FIG. 9. Internal mould of hypostoma. In.57734. ×7.

Couches du Landeyran supérieures
locality λ20, near southern end of Landeyran Valley.

FIG. 11. Internal mould of pygidium. In.57749. ×2.

Horizon as for Fig. 2.
Locality λ2, near northern end of Landeyran Valley.

FIG. 12. Internal mould of pygidium. It.261. ×2.


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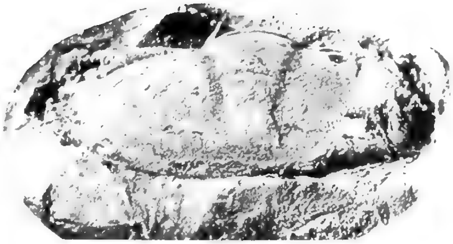
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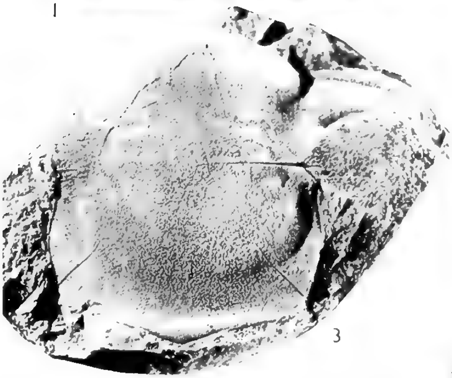
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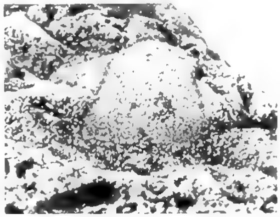
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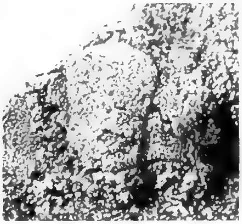
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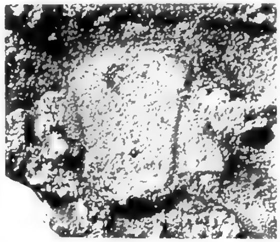
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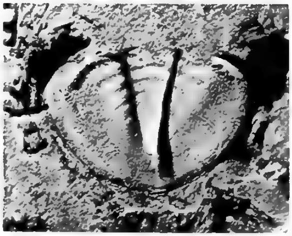
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PLATE 19

Hoekaspis? quadrata sp. nov. p. 327

Couches du Landeyran inférieures,
locality $\lambda 6$, near northern end of Landeyran Valley.

FIGS. 1, 7, 8. Latex cast of cranidium. Holotype. It.428. $\times 8$.
FIGS. 3, 5, 9. Internal mould of same specimen. $\times 8$.
FIGS. 2, 4, 6. Latex cast of small cranidium. Paratype, It.429. $\times 8$.
FIG. 12. Internal mould of same specimen. $\times 8$.
FIG. 10. Latex cast of fragmentary cranidium. Paratype, It.430. $\times 8$.

Otarion insolitum sp. nov. p. 337

Couches du Landeyran supérieures,
locality $\lambda 19$, near southern end of Landeyran Valley.

FIGS. 11, 13, 14. Anterior, left lateral and plan views of internal mould of cranidium. Holotype. In.57452. $\times 12$.

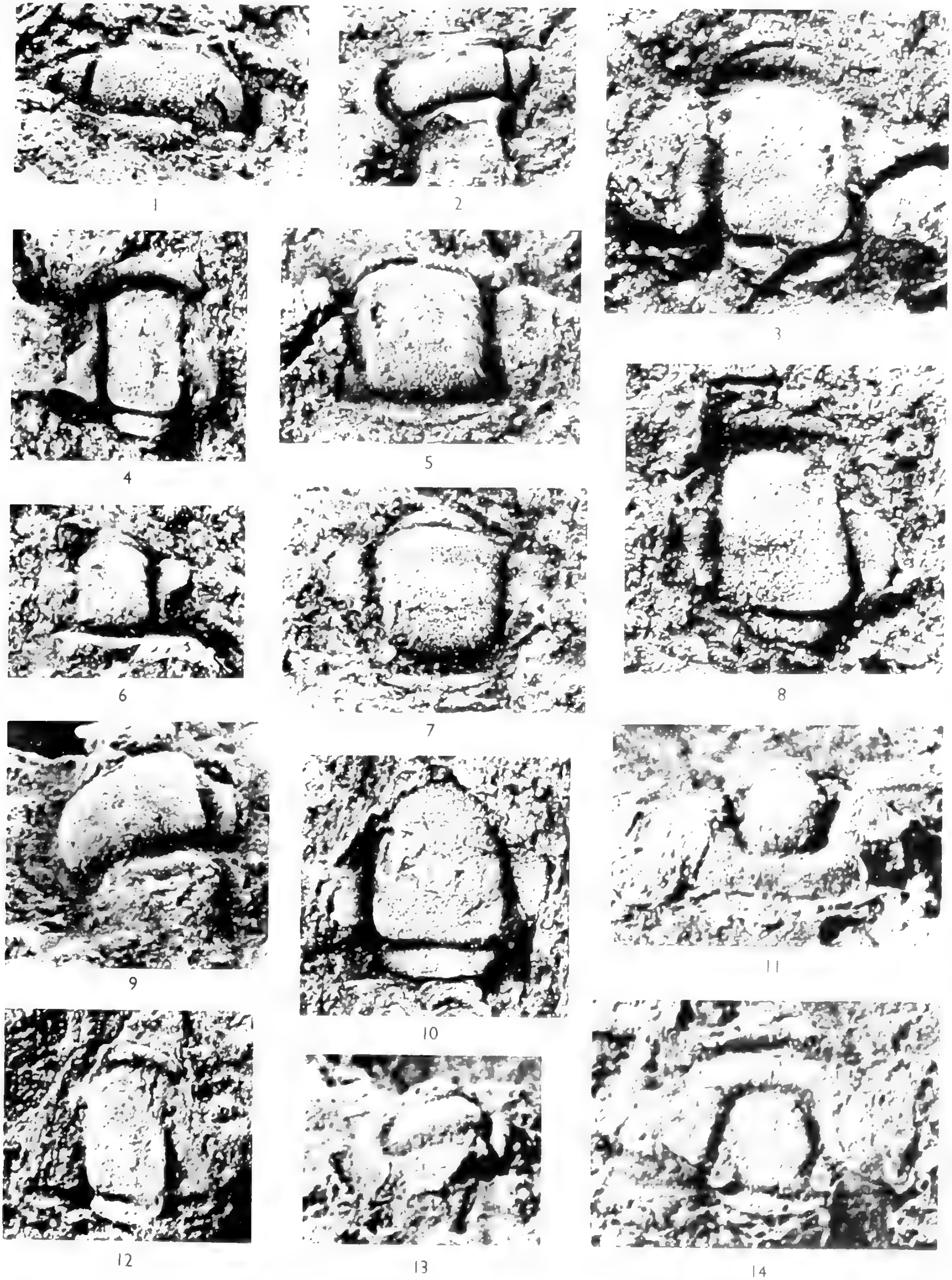
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PLATE 20

Apatokephalus incisus sp. nov. p. 339

Couches du Landeyran inférieures,
locality λ33, hillside section south-west of Le Foulon.

FIGS. 1, 2. Internal mould and latex cast of cranidium and part of thorax. Holotype, It.176. ×7.

FIG. 3. Latex cast of small cranidium. Paratype, It.177. ×9.

FIG. 6. Latex cast of thorax and pygidium with fragmentary cranidium and left librigena. Paratype, It.179, ×7.

FIG. 9. External mould of part of ventral side of pygidium. Paratype, It.183. ×3.

Horizon as for Fig. 1.
Locality λ30, hillside section south-west of Le Foulon.

FIG. 5. External mould of left librigena, slightly displaced from cranidium. Paratype, It.287. ×7.

Selenopeltis binodosus sp. nov. p. 334

Horizon and locality as for Fig. 1.

FIGS. 4, 7, 8. Plan, left anterolateral and anterior views of latex cast of cranidium. Holotype, It.180. ×5.


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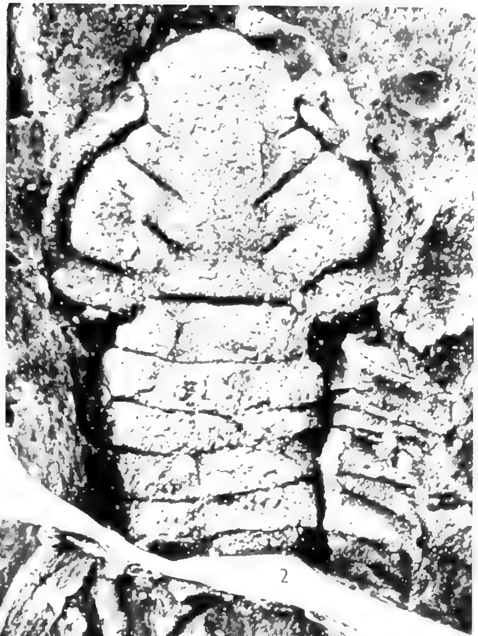
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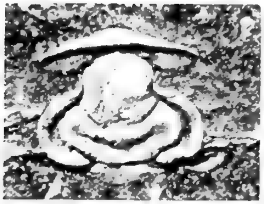
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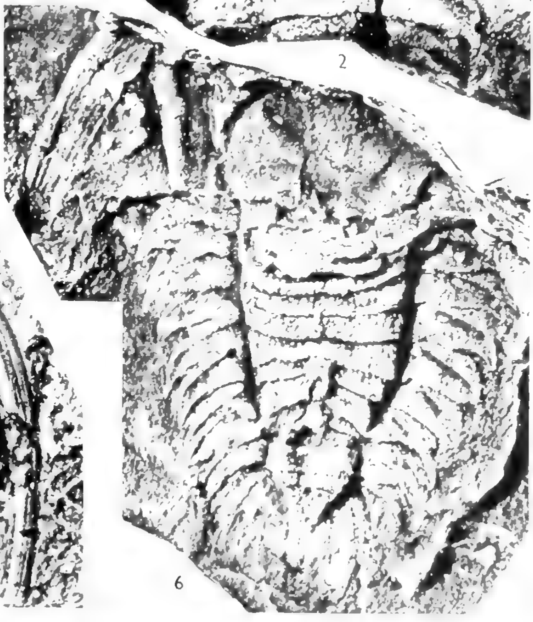
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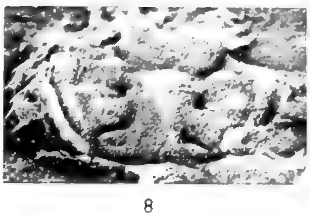
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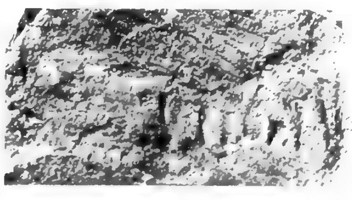
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PLATE 21

Apatokephalus incisus sp. nov. p. 339

Couches du Landeyran inférieures,
locality λ31, hillside section south-west of Le Foulon.

FIG. 1. Latex cast of cephalon showing librigenae in position. Paratype, It.181. ×8.

Horizon as for Fig. 1.
Locality λ33, hillside section south-west of Le Foulon.

FIG. 2. Internal mould of cranidium showing large lateral extension of anterior border. Paratype, It.182. ×7.

FIG. 4. Latex cast of pygidium. Paratype, It.183. ×8.

Horizon as for Fig. 1.
Locality λ2, near northern end of Landeyran Valley.

FIGS. 3, 7. Latex cast and external mould of cranidium, showing granulated surface of test, and row of pits in front of the glabella. Paratype, In.57422. ×11.

Apatokephalus? brevifrons Thoral p. 344

Arenig Series,
400 metres west of Prades-sur-Vernazobres, Hérault.

FIG. 5. Cast of holotype cranidium. University of Montpellier. ×7.

Selenopeltis sp. p. 336

Horizon and locality as for Fig. 2.

FIG. 6. Latex cast of fragmentary pleura showing long, backwardly-directed posterior pleural spine. It.184. ×3.

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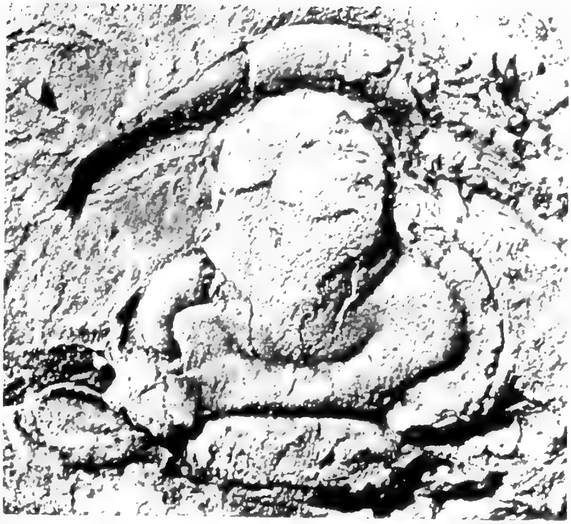

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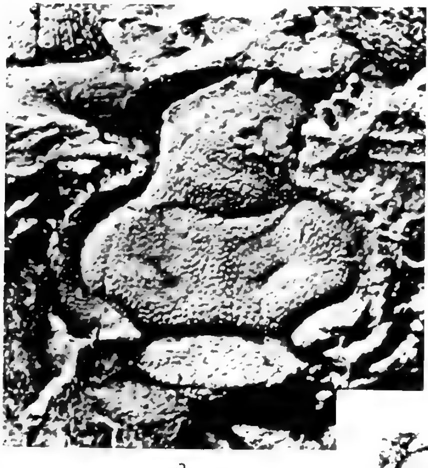

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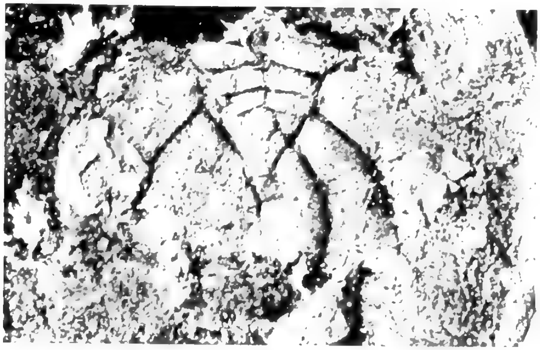

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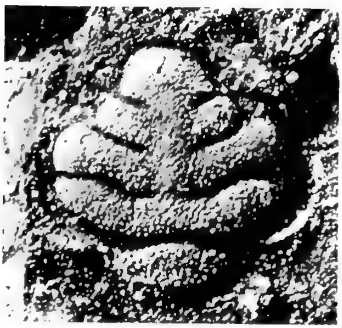

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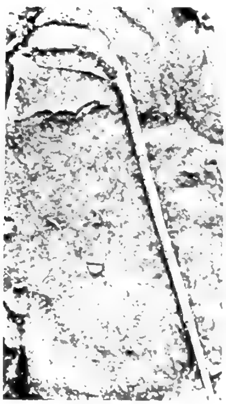

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New taxonomic names and the page numbers of the principal references are printed in **Bold** type. An asterisk (*) indicates a figure.

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